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THE UNIVERSITY OF ALBERTA

INFLUENCE OF CULTURAL CONDITIONS ON THE MORPHOLOGY OF BEGONIA LUCERNA AND OTHER BEGONIA SPECIES

by

© ELSA ERIKA MARAHRENS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

HORTICULTURE

DEPARTMENT OF PLANT SCIENCE

EDMONTON, ALBERTA

FALL, 1987

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled INFLUENCE OF CULTURAL CONDITIONS ON THE MORPHOLOGY OF BEGONIA LUCERNA AND OTHER BEGONIA SPECIES submitted by ELSA ERIKA MARAHRENS in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in HORTICULTURE.

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Date September 4, 1987

ABSTRACT

Begonias are valued by producers of pot plants because their production time is short. Therefore Flowers Canada agreed to fund 1) the investigation of cultural methods to produce compact plants of the tall *Begonia lucerna* and 2) the screening of other Begonia species for their suitability as pot plants.

All species were repeatedly grown under various light conditions. Higher temperatures than usual were tried in order to cut production time. Since an initial superphosphate application to the peat-vermiculite mix caused problems in the plants other fertilizers were tried. To produce short internodes in *Begonia lucerna* suitable growth retardants were tested at various concentrations.

Attractive plants of *Begonia lucerna* with strongly horizontal growth and an average internode length of 2.8 cm were produced with soil drenches of 0.25 mg (a.i.) ancymidol per 12 cm pot under 16 h of 18 W/m² (PAR). The same amount of ancymidol caused a much stronger reduction of internode length, on lateral shoots in particular, in *Begonia lucerna* grown in a growth cabinet under 9 h of 22.8 W/m². This was probably caused by the high proportion of far red light under the canopy of higher plants in the small cabinet. On the contrary, cycocel did not have any effect on internode elongation in this cabinet and its activity was also poor in the growth chamber. Since problems with the action of cycocel under relatively high temperatures have been reported by other workers, the 24 °C temperature is assumed to be the reason for this inefficiency.

No positive gravitropism was produced on plants in a growth chamber at 24 °C and light of 23.5 W/m² nor in a greenhouse at 19 °C with light supplemented to 16.9 mW/m² under cloud cover (maximum of 66.5 W/m² on sunny days). As expected, production time was longer at the lower temperature.

Good, marketable plants were produced with the slow release fertilizer Nutricote 14-14-14 and also in a limed medium with weekly applications of liquid fertilizer. Amendments of Osmocote 18-9-9 caused root problems, especially in the warm growth chamber.

Acknowledgement

I want to express my appreciation to the Cecil Delworth Foundation of Flowers Canada for funding this project for two years and to the Alberta Agricultural Research Trust for matching these funds. I should like to thank my supervisor Dr. E. Toop for his guidance and for promoting my independent research, thus enabling me to gain valuable experience. I am grateful to Dr. J. Robertson for his constructive criticism of the thesis, Dr. R. Knowles for his extensive assistance with the statistical analyses, and Mr. R. Kroon for sharing his vast experience in growing of pot plants.

Table of Contents

Chapter — Page

I. Introduction 1

Objectives 1

Begonia lucerna 1

Other Begonia Species 3

II. Literature Review: Growth Retardants 4

A. Daminozide 4

B. Chlorphonium 5

C. Chlormequat 6

General Remarks 6

Effect on Crop Plants and Fruit Trees 6

Physiological Observations 7

Effect on Ornamental Plants 8

Effect on Begonias 11

Chlormequat Action 12

D. Ancymidol 12

General Remarks 12

Use of Ancymidol 13

Influence of Environmental Factors 13

Media Composition and Ancymidol Action 14

Method of Application 15

Varietal Differences in Growth Inhibition 15

Influence on Flowering 16

Action of Ancymidol 16

Specific influence of ancymidol on gibberellin synthesis 16

Changes in endogeneous gibberellins 17

Inhibition of gibberellin synthesis 17

III. Literature Review: Influence of Light on Plant Growth 19
A. Photosynthesis 19
B. Photomorphogenesis 20
C. Quality of Daylight and Light under a Canopy 21
Daylight 21
Light under Vegetation Canopy 22
D. Adaption Reactions 22
Sun and Shade Plants 22
Reduced Light Intensity without Shade 24
Responses to Changes in Light Quality in Artificial Light 25
Influence of Light Quality on Apical Dominance 26
Growth Substances and Photomorphogenesis 27
E. Leaf Epinasty 28
Definition and Causes 28
Physiology of Epinasty 29
Influence of gravity 29
Ethylene and auxin 30
Gibberellins 31
Light 32
F. Plagiotropism 32
Trees and Grasses 33
Herbaceous Dicotyledons 34
Mechanism of Geotropic Bending 35
Perception phase 35
Transduction phase 36
Involvement of gibberellins in geotropic curvature 37
Model of GA-involvement in gravitropism 38

IV. Research: Strength of Growth Retardant Solutions 39
A. Introduction 39
Light 39
Preliminary Experiments 40
B. Materials and Methods 40
C. Results 41
Experiment A: Long Days 41
Experiment B: Short Days 43
D. Discussion 43
Experiment A: Long Days 43
Light requirement 43
Effects common to ancymidol and chlormequat 45
Effect of ancymidol 46
Effect of chlormequat 47
Experiment B: Short Days 48
Flowering 48
Vegetative growth 48
Effect of ancymidol 50
Effect of chlormequat 51
E. Conclusion 53
V. Research: Fertilizer, Temperature and Light 54
A. Introduction 54
Light 54
Fertilizers 54
Preliminary Experiments 56
B. Materials and Methods 57
C. Results 58

Differences between Plants in Growth Chamber and Greenhouse 58
Differences between Light Intensities 58
Osmocote 18-9-9 59
In growth chamber 59
In greenhouse 59
Plants grown in 0-20-0 Mix 60
In growth chamber 60
In greenhouse 61
Plants Grown in Medium Amended with Lime only 61
In growth chamber 61
In greenhouse 62
Plants Grown in Medium without Any Amendment 62
In growth chamber 62
In greenhouse 63
Nutricote 14-14-14 64
In growth chamber 64
In greenhouse 65
Rating 66
Summary of Results 67
Light 67
Fertilizer 67
D. Discussion 68
0-20-0 Mix 68
Unamended and Limed Growing Media 70
Nutricote 14-14-14 and Osmocote 18-9-9 71
Conclusion 74
VI. Research: Other Begonia Species Screened for Suitability as Pot Plants 76

A. Introduction 76

B. Materials and Methods 77

Descriptions of Plants 77

Propagation from Cuttings 77

Growing-on of Rooted Cuttings 77

Rooting 78

Growing-on 79

C. Discussion 80

Rooting 80

Growing-on 81

D. Conclusion 82

VII. Tables 83

VIII. Figures 88

Bibliography 98

Appendix 1: Preliminary Experiment to Establish Effectiveness of Growth Retardants on Begonia lucerna 114

Appendix 2: The Effect of Pinching to 2, 3 or 4 Nodes on Subsequent Development of Begonia lucerna 116

Appendix 3: The Effect of Various Rates of Growth Retardants on Begonia lucerna Plants Grown in 0-20-0 Mix Under Daylight Supplemented by Incandescent Photoperiodic Lighting 117

Appendix 4: Effect of Growth Retardants Combined with Low Light on Growth Response of Begonia lucerna 118

Appendix 5: Effect of Small Pots on the Development of Begonia lucerna Plants 119

Appendix 6: Effect of Various Fertilizer Treatments on the Development of Begonia lucerna Plants 120

List of Tables

Table		Page
1	Efficiency of 55% Saran Shade Mesh	83
2	Soil Drenches of Ancymidol (A-1 to A-3) and Chlormequat (C-1 to C-3)	83
3	Internode Number and Length, and Flowering under 16 h Days	84
4	Internode Number and Length, and Flowering under 9 h Days	84
5	Average Internode Number, Length, and Flowering from Tip Cuttings Grown at 24 °C (23 W/m²) for Ten Weeks after Potting	85
6	Average Internode Number, Length, and Flowering from Tip Cuttings Grown at 19 °C (±3 °C) (16 to 66 W/m²)for Ten Weeks after Potting	85
7	Average Number, Length, and Flowering of Leaf Bud Cuttings Grown at 19 °C (± 3°C) (16 to 66 W/m²) for Ten Weeks after Potting	86
8	Results of Chemical Analysis of Tissues of *Begonia lucerna* Grown in Variously Amended Media	86
9	Influence of Light on *Begonia serratipetala*	87
10	(Appendix 1) Effectiveness of 4 Growth Retardants on Average Internode Length of *Begonia lucerna*	115

List of Figures

Figure		Page
1	Untreated control plant in walk-in chamber at 12.7 W/m², 16 h days	88
2	Treatment C-1 at 165 mg (a.i.) chlormequat/pot in walk-in chamber at 12.7 W/m², 16 h days	88
3	Treatment C-3 at 260 mg (a.i.) chlormequat/pot in walk-in chamber at 12.7 W/m², 16 h days	89
4	Treatment A-1 at 0.22 mg (a.i.) ancymidol/pot in walk-in chamber at 12.7 W/m², 16 h days	89
5	Treatment A-2 at 0.25 mg (a.i.) ancymidol/pot in walk-in chamber at 12.7 W/m², 16 h days	90
6	Treatment A-3 at 0.32 mg (a.i.) ancymidol/pot in walk-in chamber at 12.7 W/m², 16 h days	90
7	Treatments A-2 and control in cabinet at 22.8 W/m², 9 h days	91
8	Treatments A-2 and C-3 in cabinet at 22.8 W/m², 9 h days	91
9	Leaf epinasty in *Begonia lucerna*, grown under daylight and 16 h incandescent light	92
10	Tip cuttings grown with Osmocote 18-9-9 in chamber at 24 °C and 23 W/m², in greenhouse at 19 °C and 16 to 66 W/m²	92
11	Tip cuttings grown with 0-20-0 in chamber at 24 °C and 23 W/m², in greenhouse at 19 °C and 16 to 66 W/m²	93
12	Tip cuttings grown with lime in medium in chamber at 24 °C and 23 W/m², in greenhouse at 19 °C and 16 to 66 W/m²	93
13	Tip cuttings grown without amendment in chamber at 24 °C and 23 W/m², in greenhouse at 19 °C and 16 to 66 W/m²	94
14	Tip cuttings grown with Nutricote 14-14-14 in greenhouse at 19 °C and 16 to 66 W/m², in chamber at 24 °C and 23 W/m²	94

15 Tip cutting and heel cutting grown with Nutricote 14-14-14 in greenhouse at 19 °C and 16 to 66 W/m² 95

16 Tip cutting and heel cutting grown with Osmocote 18-9-9 in greenhouse at 19 °C and 16 to 66 W/m² 95

17 *Begonia sp. 1301* grown in a greenhouse at 19 °C and 16 to 66 W/m² from tip cuttings, 11 weeks and 4 weeks after potting 96

18 *Begonia serratipetala* grown in a shaded greenhouse at 16 to 18 W/m², 16 weeks after potting 96

19 *Begonia serratipetala* grown in a greenhouse at 19 °C and 16 to 66 W/m², 16 weeks after potting 97

20 *Begonia sp 1302* grown in a shaded greenhouse at 16 to 18 W/m², 16 weeks after potting 97

List of Abbreviations

GA	gibberellin
HPS	high pressure sodium
IAA	indoleacetic acid
LD	long day
LSD	long-short day
NAA	naphthaleneacetic acid
SD	short day

I. Introduction

Objectives

The main aim of this work was to increase the variety or selection of marketable potted plants in Canada, since this is an area where the agricultural or horticultural market can definitely expand in the future. The potential for the pot plant market becomes obvious when the number of cut flowers and pot plants bought in one household in Europe or other parts of the world is compared to the numbers bought in Canada. The plants and flowers offered for sale in Canada have increased tremendously over the last 25 years. The willingness to buy flowering or foliage plants is still greatest for specific dates, like Christmas, Easter, Valentines Day and Thanksgiving Day, but there is a gradual acceptance that plants can be bought any time, particularly during our long winters when the eye is longing for some green in the environment. This change in attitude is easily detected in the very market conscious supermarket chains. In short, the fact that Canada Safeway Ltd., for example, sets aside increasingly larger areas in new stores for plants and flowers means that the market is expanding.

The biggest problem with potted plants in our area is the low relative humidity in the homes, particularly during the winter months. Not many species can tolerate the 15 to 25% r.h. which the manufacturers of home humidifiers recommend for outside temperatures of -10 to -30°C Therefore species have to be found which will thrive under this low relative humidity in the home heated to about 20°C.

The objective was pursued in two ways, 1) by investigating methods for mass production of *Begonia X lucerna*, a tall hybrid species which can stand such conditions and 2) by screening other Begonia species for their suitablility as pot plants.

Begonia lucerna

Begonia lucerna will survive in quite dark corners and under such low light will show good silvery spots on large dark green leaves. On the other hand it will develop large pink

flower clusters when the plant is kept in suitably higher light. These characteristics made this plant a favourite with our grandparent generation.

The problem with the species is its natural height (up to 1.80m) and cane-like stem which develops very few branches. In order to make the species acceptable for marketing, methods had to be found to produce it in a compact, attractive shape. To investigate such methods was the main purpose of this thesis.

Cane-like begonias, of which *Begonia lucerna* is probably the best known and most common, are grown commercially in small numbers only because they are large plants and need more space than most other types. They have erect, smooth bamboo-like stems with swollen nodes. The internodes are usually long and fairly even in length. Most cane-like begonias do not branch, but they do send up new shoots at the base of the plant (Thompson and Thompson, 1981).

They tolerate a wide range of temperatures, although they will grow best between 18 and 25°C. For flowering they need some sunlight, but they should be protected from midday sun in summer. They do best in 40 to 60% r.h., but do not suffer visibly when the humidity is lower, as long as it is not associated with high temperatures.

The shape of begonias can be changed by shoot decapitation, which breaks the apical dominance and encourages branching. Therefore, in order to produce plants of a manageable size a combination of pinching (decapitation) and application of growth regulators seemed advisable. Chemical growth retardants control internode elongation by inhibiting biosynthetic pathways for the natural production of gibberellins. They do not seriously disrupt the growth processes that involve chlorophyll and phytochrome (Cathey, 1975a).

Important factors dictating size and shape of plants are photosynthesis and photomorphogenesis. Photosynthesis produces the chemical energy for the synthesis of the organic components which are essential for plant growth. It is mainly determined by light quantity. Photomorphogenesis is the formative effect of light on plants. It is determined by light quality. The influence of light quantity and quality is extremely specific. Therefore it is necessary to know exactly how a plant species reacts to specific conditions in the greenhouse.

It was found that *Begonia lucerna* reacts extremely strongly to light quantity as well as to light quality. It showed not only the usual internode elongation under reduced light of the same quality, but also a seldom reported strongly lateral (horizontal) growth in the newly developing axillary branches after decapitation and treatment with growth retardants. This made it necessary to deal with the topics of geotropism and plagiotropism and the possible involvement of gibberellins in those processes. The reaction to light quality included leaf epinasty and enhanced elongation of the internodes under light with relatively high portions in the far-red part of the spectrum. These results made it necessary to deal in detail with the problem of photomorphogenesis.

Other Begonia Species

Three other begonias, *Begonia sp. 1301*, *Begonia serratipetala*, and *Begonia sp. 1302* , which had never been grown commercially, were brought in from Holland and screened for their suitability as houseplants. These species are much smaller than *Begonia lucerna* and did not require treatment with growth retardants nor pinching. They were grown first in a shaded greenhouse, similar to those used for begonia production in Europe. In order to possibly shorten production time in all three species and also to improve the weak stems in *Begonia serratipetala* these species were later grown under greater light quantities and at higher temperatures, in a greenhouse with supplemental HPS-light as well as in a 24°C growth chamber under mixed light from fluorescent and incandescent sources. These growing conditions were chosen because they can easily be produced by growers.

II. Literature Review: Growth Retardants

The use of growth regulators to retard stem elongation has become popular with commercial growers since Cathey (1959) was able to control poinsettia height. Cathey (1975b) described the action of a growth retarding chemical as delaying cell division and elongation in shoot tissue without exhibiting any formative effects. Cathey doubted that any one chemical could retard the growth of all plants and his prediction has proved accurate. In a few instances researchers and growers have witnessed growth stimulation at low concentrations of growth retardants, but in the vast majority of cases shorter plants, because of inhibition of internode elongation, have resulted from the use of growth retardants (Larson, 1985).

The mode of action of many growth regulators is still not known. Technology has preceded science in this field in many instances, and even the knowledge that the substances have an inhibiting effect on the biosynthesis of gibberellic acid does not elucidate much since the role of gibberellins in the elongation of shoots or stems is quite unclear (Jones and MacMillan, 1984). As Goodwin and Mercer (1983) point out "The involvement of GA in the process of stem elongation during normal plant growth would be more convincing if there were a positive correlation between the endogenous level of identified GAs and stem elongation." The reason for the unclarity may be that the action of GAs varies among species or even cultivars. This is supported by the findings that specific growth retardants, which are known to influence GA biosynthesis, inhibit elongation only in certain species (Cathey, 1975b) or cultivars (Seeley, 1979).

Some of the best known and commercially available growth retardants are daminozide, chlorphonium, chlormequat and ancymidol

A. Daminozide

Butanedioic acid mono-(2,2-dimethyl-hydrazide) was first researched by Riddell *et al.* (1962). It is produced by Uniroyal Chemical Co. and has become a prominent compound in floriculture under the name of daminozide or B-Nine and in pomology under the name of Alar. It is also known as SADH, kylar or aminozide. One of the reasons for its popularity is

its price, since large amounts are used on fruit trees to reduce vegetative growth and increase fruit set and yield (Jaumien, 1983; McLaughlin and Greene, 1984; and many other researchers). Alar is also used on grapes, cherries, peanuts, nectarines, tomatoes, pears, and peaches. B-Nine is recommended for growth reduction in chrysanthemums, hydrangeas, azaleas, poinsettias, gardenias and bedding plants (Thomson, 1981). On *Begonia* X *cheimantha* daminozide was ineffective (Krauskopf and Nelson, 1976).

Satisfactory explanations for its effects have not been published, although it has been reported to inhibit both GA and auxin synthesis (Larson, 1985).

B. Chlorphonium

Tributyl-2,4-dichlorobenzylphosphonium chloride is marketed under the name of chlorphonium, phosphon or CBBP by the Mobil Chemical Company. It is only recommended for ornamentals, mainly chrysanthemums and Easter lilies. It is not used widely any more since other growth retardants which are effective on a wider spectrum of species have been released. Cathey (1975a) found chlorphonium effective only on 12 out of 88 ornamental plant species tested.

Heide (1969) reported that Phosphon had no effect on growth or flowering of *Begonia* X *cheimantha* Everett; in fact, he observed that the plants had somewhat longer shoots and larger leaves than control plants at 4×10^{-4}M.

Chlorphonium is known to inhibit the biosynthesis of GA (Devlin, 1975). According to Goodwin and Mercer (1983) it inhibits the A-activity of ent-kaurene synthase, whereby the conversion of geranylgeranyl pyrophosphate to copalyl pyrophosphate is blocked. Chlorophonium also blocks the next step, the conversion of copalyl pyrophosphate to kaurene, which is a precursor in the synthesis of gibberellin.

C. Chlormequat

General Remarks

(2-Chloroethyl)-trimethyl-ammonium chloride is sold under the following names: chlormequat, CCC, cycocel, cycogan, extra, bettaquat-B, barleyquat-B and titan. It was brought out in 1964 by the American Cyanamid Company and still is very popular because of its price. Large amounts are produced for use on grain crops, such as wheat and rye, to increase the yield by increased tillering and reduced lodging (Thomson, 1981).

Effect on Crop Plants and Fruit Trees

There is a large volume of articles about the use of chlormequat from the 1980's alone, although very little from this continent. Duduk (1984, USSR) reports decreased length of the lower internodes and an increase in stem diameter, lodging resistance and yield improvement in some wheat varieties, but not in others. Rapparini *et al.* (Italy, 1984) and Bengtsson, (1985, Sweden) point out that the degree of reduction was not associated with the degree of resistance to lodging nor with grain yield after treatment of winter rye, and winter and spring wheat. Übelhör *et al.* (1984, West Germany) report a 15 year study on chlormequat-effect on oat yield, where the most important influences were on height, degree of lodging and yield. Bochniarz *et al.* (1983, Poland) found that in four perennial grasses (grown for seed) shortening of internodes increased lodging resistance and that the inhibiting effect on internode length was greater when plants were grown close together. Seed yield of alfalfa was increased by an increase in the number of primary branches (Dhaliwal and Bains, 1983, India). Strawberry plants produced more and better new plants after treatment with chlormequat. They were also more frost-resistant. GA had the opposite effect (Agafonov and Zakharova, 1985, USSR).

Chlormequat used on cotton decreased bud shedding (Ebaid *et al.*, 1984, Egypt) whereas GA application increased bud and boll abscission. Another reason for the use of chlormequat on cotton is its accelerating effect on maturity combined with inhibited stem

growth (Agakishiev and Kuzier, 1983, USSR; Saidumarov and Turaev, 1982, USSR). Promoting early maturity of shoots and frost resistance in grapes was reported by Smirnow *et al.* (1984, USSR) and Kezeli and Beridze (1982, USSR). Reducing vegetative growth and inducing early cropping in pears was achieved by Grauslund (1983, Denmark) and Houten (1985, Netherlands). Advanced fruit maturity and increased fruit set in the following years in peach was observed by Sinha *et al.* (1983, India). On the other hand, increased shoot length and delayed ripening of peaches was reported by Mansour *et al.* (1985, Egypt).

Physiological Observations

Reduced transpiration combined with retarded shoot growth in apple trees (which was counteracted by simultaneous applications of mineral fertilizers) was reported by Kornesku (1983, USSR). The use of chlormequat during drought, because of increased relative water content, was recommended by Balasimha and Subramonian (1984, India) on cacao seedlings and on *Cyamopsis tetragonoloba* (cluster beans) by Vaid *et al.* (1983, India).

Decreased shoot height, increased root dry matter, but no effect on leaf number and area in *Vicia faba* (broad bean) was reported by Abdul and Said (1984, Iraq), whereas GA_3 increased plant height, leaf number, leaf area and shoot dry weight. On the other hand, stem elongation by 10 to 100 ppm chlormequat sprays on *Vicia faba* was reported by El-Beltagy *et al.* (1979, Egypt).

In *Phaseolus vulgaris* (bean) seeds treatment with chlormequat before sowing resulted in a decrease of free gibberellins in the growing shoot, whereas the total amount of gibberellins remained unaffected (Nagy and Tabi, 1982, Hungary). Those authors conclude that the effect of chlormequat occurs through increased membrane permeability. In *Datura innoxia* (a pharmaceutical plant) chlormequat reduced the effect of salinity, namely growth retardation and alkaloid content depression (Awad *et al.*, 1983, Egypt). According to Mostafa *et al.* (1984, Egypt) chlormequat modifies the inhibitory effect of salinity on cambium activity. The latter authors also observed enhanced conductive tissue differentiation in the leaf midrib, more cells and decreased intercellular spaces in the leaf and more and wider

xylem vessels and phloem elements in secondary roots.

Effect on Ornamental Plants

Very differing results by chlormequat on ornamental plants are reported. Unfortunately, often the growing conditions are not mentioned. On *Anisodontea capensis* 0.5% in the irrigation water was effective, whereas on *Cestrum purpureum*, a long-short day (LSD) plant, which requires a long day (LD) period followed by short days (SD) for flowering, did not react (Bleser *et al.*, 1985, Germany). Reimherr (1984) found in addition, that *Anisodontea capensis* flowered earlier when treated with chlormequat. *Antirrhinum majus* L (snapdragon) was found to produce more flowers after chlormequat treatment (Sarhan and El Sayed, 1983, Egypt), whereas GA_3 produced the largest flower stems. Cathey (1975) had reported that a different cultivar of snapdragon did not react to chlormequat. *Campanula carpatica* grown in pots for flowering plants in spring under 16 h light produced shorter internodes after a 0.1% chlormequat spray than without treatment (Schmidt and Brundert, 1981, Germany). On carnation 0.25% chlormequat produced more large flowers only when 18 h days were provided, whereas 0.5% chlormequat reduced the flower production (Bylov and Smirnova, 1984, USSR). Yonemura (1980, Japan) found that 40 mg chlormequat/pot applied 10 days after pinching resulted in the optimum retarding effect in carnation cv. Piccadilly.

In *Chamaelancium uncinatum* chlormequat substituted for four weeks of SD which are normally required for flowering. GA sprays or LD treatment under otherwise flower-inducing fall conditions reduced the number of flowers per plant (Shillo *et al.*, 1985, Israel). Foliar sprays of 1500 mg chlormequat/ℓ water were found to be ineffective on chrysanthemum (Reed and Nightingale, 1983, USA) whereas Cathey (1975a) reported that a spray with 1000 ppm chlormequat was effective. Reduced internode length in chrysanthemum was also reported by Bachthaler and Jansen (1985, Germany), but they point out that temperature had a greater effect on growth as well as on flowering. Increase in stem length under rising temperatures (to 24 °C) was reduced more by SADH than by chlormequat at

0.6%.

In *Gladiolus* chlormequat and SADH increased flower size, whereas GA_3, IAA and NAA increased the numbers of flowers per spike (Battacharjee, 1984, India). In *Hydrangea macrophylla* transpiration and wilting were reduced more by an antitranspirant (Elvanol) in conjunction with chlormequat than without chlormequat (McDaniel, 1985, USA). In *Hibiscus rosa-sinensis* cultivars differed, requiring slight, moderate or great quantities of chlormequat for the production of compact plants and good flowering (Beuzenberg, 1982, Netherlands). Reduced length of internodes, lasting for three years, on several *Hibiscus* species as well as other woody Malvaceae, such as *Alyogyne heugelii, Lavatera plebeia* and *Gossypium sturtianum* were reported by Sedgley *et al.* (1981, Australia). In *Jasminum grandiflorum* chlormequat and B-9 induced early flowering and retarded vegetative growth (Battacharjee, 1983,India, 1983). On *Lilium tigrinum* Battacharjee (1984) found reduced height and improved flowering after spraying with 2500 ppm chlormequat (also with 2500 ppm SADH). Cathey (1975a) reported no effect on *Lilium longiflorum* Thumb. In *Lychnis* triple sprays of chlormequat reduced growth slightly, but at 0.8% it damaged the leaves, whereas SADH was not effective (Zimmer and Gebauer, 1984, Germany).

In *Mathiola incana* (stocks) and *Althea rosea* (hollyhock) chlormequat at 1500 mg/ℓ decreased plant height and length of inflorescences, but increased the number of lateral shoots, inflorescences and flowers; it also advanced flowering. GA_3 at 60 mg/ℓ increased shoot growth, but had no effect on inflorescences or flowers (Hamza and Helaly, 1983, Egypt). In *Tagetes erecta* moderate growth reduction and an increase in flowers per plant at 500 ppm chlormequat or 750 ppm TIBA were reported by Parmar and Singh (1983, India). Cathey (1975a) also found chlormequat effective on this species.

In *Pelargonium hortorum* (Geranium) chlormequat was found to be effective by Cathey (1975a). Since geraniums are produced in great masses for small and large containers in sunny locations many researchers have tried to find methods to keep them compact when the hours of sunlight are still short. All workers reported reduction of internode length at repeated 1500 ppm chlormequat sprays or one 2400 ppm soil drench, whereas the influence on

flowering date seemed to vary. Advanced flowering was reported by Miranda and Carlson (1980, USA), Sytsema (1984, Netherlands), Bachthaler and Jansen (1982, Germany) and Vinceljak-Toplack (1983, Yugoslavia). White and Warrington (1984a, 1984b, New Zealand), however, found no effect on flowering date by chlormequat, whereas a rise in the daily mean temperature from 16 °C to 18 °C or 20 °C, accelerated flowering. White and Warrington (1984b) found a decrease in starch and sugar levels in leaves when temperature increased. All authors report that flower and inflorescence sizes were reduced, but the number of flowers was increased by chlormequat. Variations among cultivars in the effect on flowering date are reported by Schwartz *et al.* (1985, USA). Miranda and Carlson attribute their result of advanced flowering to a reduced light requirement for flower induction, as had been postulated by Jansen (1973). Armitage *et al.* (1984, USA) reported that in geraniums chlormequat treatment increased photosynthesis, transpiration and chlorophyll concentration and reduced photorespiration for several days after treatment. No interaction between chlormequat and shade level was found by Schwartz *et al.* (1985, USA). In treated and untreated plants height increased with the level of shading, whereas the number of flowers decreased, but the effect of chlormequat was greater in one cultivar than in the other.

Poinsettias (*Euphorbia pulcherrima*) are one of the main crops for which chlormequat is recommended by its producer. Cathey found as early as 1959 that poinsettias reacted to chlormequat. Shoot length was reduced most effectively during the three weeks following the second (1500 ppm) spraying, then development proceeded as in untreated plants, but final height was reduced by almost 30% according to Kuack *et al.* (1982, USA). Kuack and Tayama (1983) found that foliar sprays (2 times) were more effective than soil drenches of as high as 3000 ppm. Brundert and Schmidt (1983, Germany) recommended eight sprayings with 0.25% chlormequat, because soil drenches of 250 mℓ/pot with 1% chlormequat gave unshapely plants of low quality. Hendriks and Brandis (1981, Germany) even recommended 8-10 weekly sprayings with 0.25% chlormequat at 100-150 mℓ/m^2, i.e. about 12 pots, to produce a medium sized plant. Hendriks and Brandis (1982) observed that the effect of chlormequat was strongest at low nitrogen rates. But the best quality plants were achieved

with nitrogen applications as high as the plants would take up (700 mg N/plant) combined with fortnightly, weekly or twice weekly sprayings to produce the wanted size of plant. Barrett and Nell (1982, Florida) found that total plant transpiration was reduced by 12% from 495 mg chlormequat/pot and by 24% from 0.5 mg ancymidol/pot.

Effect on Begonias

On *Begonia* species the first report about treatment with chlormequat came from Heide (Norway, 1969), who found it effective on *Begonia* X *cheimantha* Everett (Christmas begonia) at 18 °C, but not at 21 and 24 °C with 2 x 10^{-2}M (2140 mg) chlormequat per pot. With 5 x 10^{-3}M (535 mg/pot) growth was even stimulated at the higher temperatures. The plants were grown in 8 h daylight and 16 h weak photoperiodic supplementary light of 100 to 150 lx from incandescent lamps. The chlormequat treated plants flowered much earlier and better than untreated plants. Heide found the level of extractable auxin reduced by chlormequat treatment and attributes this to reduced gibberellin activity, since in several plants gibberellin had been shown to stimulate some steps in the biosynthesis of auxin. But he also mentioned the possibility that chlormequat may also act directly by increasing auxin catabolism, as Gaspar and Lacoppe (1968) had suggested. Heide thought that the high auxin level in Begonia plants grown at high temperatures was probably the reason for the reduced growth retarding effect of chlormequat with increasing temperature.

Krauskopf and Nelson (1976) treated *Begonia* X *hiemalis* Fotsch. (Rieger Elatior begonia) with 0.3% a.i. in 180 mℓ soil drench per pot and found this excessive on winter grown plants, whereas neither 0.3% nor 0.6% were effective on a summer grown crop. Krauskopf and Nelson attribute this to the respective low and high light intensities. The same authors found a 0.3% spray of about 15 mℓ chlormequat solution effective, but observed some foliar chlorosis.

Wikesjö and Schüssler (1982) also recommended chlormequat sprays of low concentration, 0.08%, two or three times, in winter and four to five times in summer. Schenk and Brundert (1980) tried to improve the quality of Rieger Elatior begonias which were grown in

winter quite closely together and had long and soft internodes. They sprayed four weeks after potting with 0.05% or 0.075% chlormequat two or three times and found the effect too strong. In plants treated twice and in plants treated three times marginal necrosis was detected on the leaves. Small Rieger begonias were produced by v. Hentig and Knösel (1981, 1984) spraying the plants with 0.15 or 0.3% chlormequat once at the beginning of a short day treatment. Holcomb (Pennsylvania, 1979) found chlormequat effective on Rieger begonias, when applied as a spray or as a soil drench at 3000 ppm at 18 °C under natural days extended by low intensity incandescent light from 6 to 12 p.m.. Holcomb did not experience the excessive retardation reported by Krauskopf and Nelson. (The reason for this result might be Holcomb's 4" pots which would not hold much drench).

Chlormequat Action

According to Goodwin and Mercer (1983) chlormequat prevents GA_3 synthesis in the same way as chlorphonium does, it blocks the conversion of geranylgeranyl pyrophosphate to copalyl pyrophosphate by inhibiting the A-activity of ent-kaurene synthase. Unlike chlorphonium, chlormequat is specific to this one step in gibberellin biosynthesis and does not affect the following one. The idea of Gaspar and Lacoppe (1968) that chlormequat may also act directly on auxin catabolism does not seem to be proven.

D. Ancymidol

General Remarks

α,-cyclopropyl-α-(4-methoxyphenyl)-5-pyrimidinemethanol) was brought out in 1971 by Elanco Products Co. and is also known as A-Rest, ancymidol or reducymol (Thomson, 1981). This growth regulator, first called EL 531, was identified in 1970. The commercial retardant was to be named Quel, but this name was not approved and the compound was named A-Rest (Larson, 1985).

Ancymidol controls the height of numerous floricultural crops. Cathey (1975) found that 68 out of 88 ornamental species reacted to it, by far the highest number of the five growth retardants he compared. Nevertheless, it has not been widely accepted by commercial growers. Larson (1985) thought the reason may be that the growers are loyal to the older substances, like chlormequat and daminozide, or the fact that some species are extremely sensitive to low concentration of commercial A-Rest, although it is marketed at 0.026% a.i. (compared to 11.8% chlormequat). The main reason, again, is probably the very high price, because it is almost exclusively recommended for ornamental crops.

Use of Ancymidol

The only non-ornamental on which ancymidol seems to have been used is asparagus transplants. Adler *et al.* (1985) found that 0.5 ml/plant applied to 7.5 week old plants enhanced production of stocky, compact transplants. If applied to younger (3.5 week old) plants it increased the partitioning of dry matter into fern rather than crowns.

Ancymidol is widely used on bedding plants to produce and keep compact plants. According to Carlson (1980) all common ornamental bedding plants with the exception of *Viola* and *Gomphrena* will respond.

Ancymidol was found ineffective only on a very few potted ornamental plants. No effect was found by Adriansen (1980) on *Paphiopedilum* (an orchid), where ethephon was the only retarding substance found. Very little effect was reported by Barrett and Nell (1984) on *Ficus benjamina*, but this might have been due to the 80% light exclusion in the shade house conditions which would strongly promote stem elongation. Although it could be expected that the very high dose of 10 mg ancymidol/pot would be able to counteract this.

Influence of Environmental Factors

When low light levels increased plant size absolute height reduction through ancymidol was observed to be greater, although the percent height reduction remained about the same as under higher irradiances in *Lilium longiflorum* (Weiler, 1978) after treatment with

0.5-0.75 mg/pot ancymidol as soil drench. Similar results were reported by Williams *et al.* (1986) on Easter lilies with longer internodes caused by short periods of fluorescent and incandescent supplemental light.

On Rieger begonias Krauskopf and Nelson (1976) found a soil drench of 0.125 mg ancymidol/pot effective under high as well as under low (natural) light conditions, supplemented by 4 hours of 108 lx incandescent light to prolong the photoperiod. This result was in contrast to their results with chlormequat which caused excessive height retardation at 0.3% drench in a winter grown crop and had no effect on begonias grown in summer. Holcomb (1979) reported good height control in Rieger begonias by ancymidol as well as by chlormequat under naturally short days and 17 °C night temperatures.

Hanks and Menhenett (1983) reported that ancymidol (0.312-2.5 mg/pot) dwarfed early and mid-season forced tulips more than late-season crops. This was particularly so when the (outdoor) temperature following the cold treatment was relatively high. Hanks and Menhenett, therefore, argue that under the higher temperature greater GA-mediated stem growth occurred before treatment, and ancymidol could not block this growth response because it was already under way.

The only apparent interaction between ancymidol and photoperiod, causing increased height in one cultivar of Easter lilies, was reported by Roh and Wilkins (1977). This happened when ancymidol was applied once or twice (but not when it was applied three times) to lilies kept under 21 °C day and 15 °C night temperature under normal day length with the photoperiod extended by 432 lx incandescent light for 8 hours. Roh and Wilkins (1977) hypothesize that the extended photoperiod may have increased the potential of gibberellin synthesis.

Media Composition and Ancymidol Action

The growing medium was found to influence the effectiveness of ancymidol. Larson *et al.* (1974), Tschabold *et al.* (1975), Bonamino and Larson (1978) and Barrett (1982) found that 0.25 mg ancymidol/pot was effective on *Chrysanthemum morifolium* in all media

except pine bark humus, where three times that amount was needed. Incorporation of riversand or greenhouse soil to pine bark increased effectiveness, as did incorporation of $Ca(OH)_2$. Larson *et al.* (1974) explain that the ancymidol may be tied up in pine bark, because its ammonium radical may form a union with pine bark particles.

Method of Application

Soil drenches were more effective than foliar sprays on *Chrysanthemum* (Larson, 1974). Holcomb *et al.* (1983) had to use 2500 mg ancymidol/ℓ spray solution compared to 0.25 mg/pot in soil drench to achieve the wanted growth retardation in *Chrysanthemum*. Menhenett (1984) reports very little action of ancymidol sprays in low concentrations (also on *Chrysanthemum*). Wilfret (1981) did not achieve the desired growth retardation on pixie poinsettas by foliar sprays of ancymidol.

Soaking of entire rooted cuttings in 50 mg ancymidol/ℓ water for 60 seconds resulted in excessive growth reduction and delay in flowering, whereas soaking in daminozide solutions gave the desired results (McDaniel and Fuhr, 1977). The authors attributed the greater dwarfing effect to more rapid absorption and translocation.

Various fertilizer levels produced differences in stem length in *Dieffenbachia maculata* (Joiner *et al.*, 1978). But ancymidol and fertilizer levels acted independently on growth response; thus increasing fertilizer did not overcome the dwarfing effect of ancymidol.

Varietal Differences in Growth Inhibition

Differences in the reduction of internode elongation not only among species, but also among cultivars, grown under the same conditions, were reported for garden lilies, grown as potted plants (Seeley, 1982; Staden and Maas, 1980), for forced tulips (Hanks and Menhenett, 1983) and for dahlias (De Hertogh and Blakely, 1976).

Influence on Flowering

Although no influence on flowering by ancymidol is reported for many plants in some species or cultivars it may advance and enhance or delay and reduce flowering. Both reactions are combined with stem growth inhibition. Delay in flowering was reported for some tulip cultivars (Menhenett and Hanks, 1982/83, Suh *et al.*, 1983), for some Easter lily cultivars (Hammer and Kirk, 1981; Lewis and Lewis, 1982), for *Schlumbergera truncata* (Christmas cactus) (Ho *et al.*, 1985), for Chrysanthemum (Menhenett, 1984) and for one of two *Aeschynanthus* species (Adriansen and Andersen, 1983). On the other hand, advanced and enhanced flowering was caused by ancymidol treatment in geranium (Miranda and Carlson, 1980), in poinsettias (Kolza *et al.*, 1982), in *Schizanthus* (Bridgen *et al.*, 1982) and in *Clerodendron ugandense* (Zimmer and Pöttger, 1981).

Action of Ancymidol

Specific influence of ancymidol on gibberellin synthesis

Koranski *et al.* (1979) investigated the influence of ancymidol, which is known to inhibit GA_3 synthesis, on growth and flowering of the strongly responding *Clerodendron thomsoniae*. Ancymidol greatly retarded stem elongation and markedly increased flowering under inductive conditions, while treatment with GA_3 stimulated vine growth and prevented flowering. In contrast to GA_3, treatment with GA_7 had little effect on vegetative growth, but increased flowering under inductive conditions. The level of gibberellin-like substances determined by bioassay, were increased in ancymidol-treated Clerodendron. Koranski *et al.* therefore concluded that ancymidol may be specific for each gibberellin, i.e. it may decrease the synthesis of GA_3 and thereby affect the vegetative growth, while simultaneously promoting the synthesis of other gibberellins, such as GA_7 and thereby promote flowering. Koranski *et al.* take as further support for their theory that the effect of ancymidol on vegetative growth was not strongly influenced by the environment, but its promotive effect on flowering was dependent on an inductive environment.

Changes in endogeneous gibberellins

Okubu and Uemoto (1985) investigated the changes in gibberellin content in tulip stems which were either rapidly elongating because of dark treatment or were inhibited from elongating by ancymidol. They found that during the elongation-promoting dark periods the amounts of free gibberellins and diffusable auxin increased, while bound gibberellin decreased. In light the free gibberellin and diffusible anxin decreased, while bound gibberellin increased. Ancymidol application prior to the dark treatment inhibited the increase in free gibberellin and diffusible anxin. Application of GA_3 increased both elongation of the stem and the amount of diffusible anxin. It also caused recovery from ancymidol-mediated reductions in elongation and diffusible auxin content.

After excision of all organs above the first internode dark-induced elongation was inhibited, also free gibberellin increased and bound gibberellin decreased. The dark treatment resulted in internode elongation only when IAA was applied. Elongation also occurred without dark treatment when GA_3 and IAA were applied. Okubo and Uemoto (1985) therefore argue that the dark-induced elongation of tulip stems is promoted by auxin, which is transported from the upper organs into the stem as a result of stimulation from the dark-induced increase in free gibberellin.

Inhibition of gibberellin synthesis

Even Obuku and Uemoto state that next to the conversion of bound to free gibberellins in dark-induced elongation of tulip stems there is also an increase in gibberellin which can be blocked by ancymidol. This inhibition of gibberellin synthesis by ancymidol was researched by Coolbaugh and Hamilton (1976). Coolbaugh, Hirano and West (1978) found that ancymidol is a very potent, specific inhibitor of all three steps in the sequence ent-kaurene → ent-kaurenol → ent-kaurenal → ent-kaurenoic acid in the gibberellin biosynthesis pathway. These steps are all oxidations catalysed by cytochrome P450 mixed function oxygenases. According to Goodwin and Mercer (1983) it is thought that ancymidol interacts with the cytochrome P450 component.

This interaction may involve the binding of one of the pyrimidine nitrogen atoms for the protohaem Fe of cytochrome P450, thereby preventing the binding of oxygen to it.

III. Literature Review: Influence of Light on Plant Growth

The three light requiring processes governing plant growth are photosynthesis, photomorphogenesis and photoperiodism.

A. Photosynthesis

Photosynthesis is the most important of the light requiring processes because radiant energy is converted into chemical energy which is necessary for the synthesis of the organic compounds from which the plant is built. Minimum irradiation levels for photosynthesis, vary between species, but are typically between 5 and 20 W/m^2 or 2000 to 8000 lx, which generally calls for high-intensity-discharge lamps in artificial lighting. The photosynthetic action spectrum has a maximum in the red area at about 675 nm with a lesser one in the blue at about 455 nm and a minimum in the green near 520 nm (Anon. 1982)..

But the most important requirement for artificial lighting for photosynthesis is, in practice, that it should contain a high proportion of its energy in the wavelengths between 400 and 700 nm. Differences in the rate of photosynthesis is more likely to be the result of other environmental factors than of spectral distribution in the artificial light used (Vince-Prue and Canham, 1983). Therefore, for optimum growth, factors such as temperature, humidity and nutrients should be appropriate to the level and time of irradiation.

On the other hand, because of the peak of the sensitivity curve for photosynthesis at 675 nm some authors think that some lamps are more effective than sunlight, since their energy is concentrated in the area of maximum sensitivity. But lamps emitting wave lengths exclusively around 675 nm would cause excessive elongation at the expense of formative growth (Anon. 1982).

The quantity of light necessary to achieve adequate rates of photosynthesis is considerably in excess of that required for normal photomorphogenesis. Plant growth is satisfactory at 30 to 60 W/m^2 for a 12 hour day or 1.25 to 2.50 MJ/m^2 per day. During the darkest weeks just north of London, which is only three degrees further South in latitude than Edmonton, inside the greenhouse an average of 0.85 MJ/m^2 per day (which translates into

18 W/m² photosynthetically active radiation for 12 h per day) have been measured by Vince-Prue and Canham, 1983). This is still far in excess of the irradiation needed in photomorphogenesis to saturate the low energy reaction (10 W/m² for 200 sec) as well as the high irradiation response at 4.0 W/m² of blue light (Furuya, 1968, Turner, 1969, Vince-Prue and Canham (1983.)

B. Photomorphogenesis

The term photomorphogenesis today includes all regulatory effects of light in the range of about 300 to 800 nm on the development of plants, independent of photosynthesis (Schopfer 1984, Street and Oepik,1984). On the contrary Mohr (1978) thought that definition too broad and gave his own as a non-directional developmental response to a non-directional, non-periodic light stimulus. All authors seem to agree that photomorphogenesis is a specific adaptation of the autotrophic plant which is forced to cope with greatly variable light conditions in its natural environment in order to optimize the chances of survival (Schopfer, 1984). Secondly, all authors consider phytochrome as the most important sensor pigment for the detection of photosignals from the environment and for making use of this information to regulate the orderly development of the living system (Mohr, 1978). The developmental effects of complete darkness is called skotomorphogenesis (Mohr, 1983). Photomorphogenesis and skotomorphogenesis are the extremes of a wide range of quantitative developmental adaptations to light, rather than all-or-none strategies (Schopfer, 1984).

Phytochrome activity in normal green plants exposed to white light is not easily studied because green plants are dependent on light as an energy source for photosynthesis. Because of the unavoidable interference with photosynthesis the adult green plant and its organs are complex and experimentally cumbersome objects for the investigation of the mechanisms of photomorphogenesis (Schopfer, 1984). Therefore most functional aspects of photomorphogenesis have been studied in young, dark-grown seedlings which are capable of rapid development on the basis of their own stored nutritional reserves. It is not clear how much of these results gained with hypocotyls can be used for light-grown plants.

The phytochrome system enables a plant to sense the spectral composition of light. Under illumination of a mixed spectrum phytochrome assumes a photostationary state in which the ratio of P_r:P_{fr} is determined by the proportion of different wavelengths in the light (Morgan and Smith, 1976). The generalized effect is that plants growing exclusively under red light look spindly and have small leaves. This appears to be the result of a lack of blue light. For most species the amount of blue light necessary for normal growth is so small that the daylight entering a greenhouse will be sufficient (Meijer, 1971).

C. Quality of Daylight and Light under a Canopy

Daylight

As long as the sun is more than 10° above the horizon, the spectrum of the global radiation is relatively constant. A typical spectral distribution curve of daylight under a clear midsummer sky has peaks in the blue and blue-green bands and, gradually, declines in the longer wavelengths (Street and Öpik, 1984, Anon. 1982). Clouds as nonselective diffusing filters lead to a small increase in blue (scattered) light, but little modifications at longer wavelengths (Holmes and Smith, 1977; Robertson, 1966). But clouds can have very large effects, up to 90% reduction, on the total photon flux in the visible light. Dust or haze in the atmosphere tends to increase the relative amounts of red light and reduce the blue in a typical daylight spectrum (Robertson, 1966).

The R:FR ratio (photon flux on 655 to 665 nm/photon flux on 725 nm to 735 nm) is important because these bands are centered around the known absorption maxima of phytochrome. R:FR in daylight was found to be only very slightly affected by climatic or cloud conditions (Holmes and Smith, 1977). At latitude 53° N during daylight R:FR was found to average 1.15 ± 0.002 irrespective of time of year or of weather conditions. In twilight (solar elevation between +10° and -10°) spectra were found to be rich in blue from the high amount of scattered skylight because of the increasing path length through the earth's atmosphere. The far-red portion is also high because of high atmospheric refraction, whereas twilight is

relatively poor in the orange-red waveband. On a cloudless day (R:FR ≃ 1.15) there may be a drop to 0.8-0.7 at dusk (Smith, 1982).

Light under Vegetation Canopy

Under canopies radiation consists of unfiltered solar radiation, direct and diffuse, which has passed through gaps in the vegetation and of filtered radiation which has passed through the vegetation and has there been partially absorbed, reflected and scattered. Away from sunflecks the spectrum is greatly influenced by absorption by photosynthetic pigments which reduces the photon flux rates in the blue and red wavelengths to very low, with a small peak in the green and a large peak in the far-red area (Holmes and Smith, 1977). The R:FR ratio under vegetational shade was found to be 0.2-0.5 in a wheat field and 0.49-0.74 under a stand of oaks (Smith and Morgan, 1983).

D. Adaption Reactions

Sun and Shade Plants

In established plants two basic responses to shade are observed: avoiding the shade (through photomorphogenic response) or tolerating it (photosynthetic response). The 'shade avoiders' redirect their development in shade to internode extension at the expense of leaf development, thereby keeping the young leaves out of the shade. The 'shade tolerators' change to a highly efficient utilization of resources and low growth rate. Therefore structural and biochemical changes occur in these plants which enhance the efficiency of photosynthetic energy transduction and reduce respiratory losses (Smith, 1982).

Great differences exist in the light dependence of photosynthesis between sun plants and shade plants. In shade plants at low light intensity the rate of net photosynthesis is considerably higher than in sun plants because of the low rate of dark respiration. However, light saturation is also reached at a lower light intensity in shade plants. Shading of sun plants, as a rule, results in a strong decline in photosynthetic rates compared to light saturated

conditions as well as in a decline in the rates of dark respiration. Björkman (1981) found in a sun plant (*Atriplex triangularis*) grown at one tenth of the usual photon flux a reduction of 80% in both rates compared to plants grown under the usual sunny conditions. But the dark respiration and photosynthesis rates of sun plants grown near their shade tolerance limit are still much higher than in shade plants. Shade plants, on the other hand, have an intrinsically low potential for photosynthetic light acclimation. They have a high susceptibility to light injury. But, as Björkman (1981) points out, part of the problem may be related to correlated factors, such as adverse water relations.

The most common morphogenic reactions are changes in leaf physiology and stem elongation. Studies on identical genotypes grown under different light regimens, and comparisons between sun and shade leaves of the same individual plant, have demonstrated that the light response characteristics of a plant or individual leaf may strongly be modified by the growth light regime (Björkman, 1981, Morgan and Smith,1982). Larger and thinner leaf blades are the most obvious features of leaves grown in shade. Shade leaves have a thinner cuticle and a much less developed epidermis which lets the green appear brighter. The mesophyll has round and irregular palisade cells, contrary to the high proportion of long columnar cells in the palisade parenchyma of sun leaves, which often develop an additional layer of palisade cells. Shade leaves also generally have more chlorophyll on a weight basis, especially chlorophyll b, because each chloroplast has more grana than those of sun leaves. In some shade plants thylakoids are more highly developed in the grana. Chloroplasts in leaves growing in shade are arranged along the cell walls in patterns that maximize light absorption (Björkman, 1981; Salisbury and Ross, 1984).

Seedlings of the following dense grassland species elongated rapidly under shade: *Arrhenatherum elatius* (oat grass), *Betonica officinalis, Rumex acetosa* (dock) and *Plantago lanceolata* (plantain). Initial height growth was negligible under shade in herbaceous species which are restricted to low turf and bare soil, such as *Arenaria serpyllifolia* (sandwort), *Hieracium pilosella* (hawk-weed) and in trees which are pioneers of abandoned arable land, such as *Betula populifolia, Betula lenta* and *Rhus glabra* (Grime and Jeffrey, 1965).

The only potted plant on which shadelight was reported to cause taller growth in close spacing were seed geraniums. Miranda and Carlson (1980) attributed this to the lower R:FR ratio.

Reduced Light Intensity without Shade

According to Smith (1982) a large body of work has shown incontrovertibly that morphogenic reactions occur in response to reduction in the total photon fluence rate (constant spectrum). In some, but by no means in all species reduced light levels caused increased stem extension as a shade-avoidance reaction, but the most general responses seem to be changes in leaf size and structure, in chloroplast number, distribution and structure and in photosynthetic and respiratory metabolism analogous to those seen in shade-tolerating species in nature.

Blackman and Wilson (1951) demonstrated that decreasing light intensity below full daylight increased the ratio of leaf area to plant weight, the ratio of leaf area to leaf weight, and the proportion of stem for *Scilla non-scripta* although the net assimilation rate increased with light intensity. Blackman and Wilson (1951) reported the same changes in *Helianthus annuus* (sunflower), *Fagopyrum esculentum* (buckwheat), *Trifolium subterraneum* (clover), *Tropaeolum majus* (nasturtium), *Lycopersicon esculentum* (tomato), *Vicia faba* (broad bean), and *Geum urbanum*.

In the production of potted plants the influence of light quantity has been reported in recent years mainly in geraniums and Easter lilies. Geraniums grown from seed as well as from cuttings were found to increase in height under shade mesh, which only changed light quantity (Schwartz *et al.*, 1985). Under 30% shade the difference in height was small, but under 63% shade height increased up to 62%. In *Lilium longiflorum* Weiler (1978) reported that low light levels increased plant size. Wilkins *et al.* (1986) reported that height of lilies was increased significantly by reduced light duration (4 h compared to 8 h), as well as reduced light intensities (4 h of 300 μmol $s^{-1}m^{-2}$ resulted in 96 cm height, 4 h of 400 μmol $s^{-1}m^{-2}$ in 66 cm; 8 h of 300 μmol $s^{-1}m^{-2}$ produced 53 cm stems, 8 h of

400 μmol $s^{-1}m^{-2}$ 45 cm stems). In *Pelargonium* X *hortorum* White and Warrington (1984) found high light to reduce leaf area and to keep plants compact.

Responses to Changes in Light Quality in Artificial Light

Downs *et al.* (1957) were the first to demonstrate red/far-red (R:FR) reversible control of stem development in light-grown plants. Five minutes of FR at the end of 8 hrs of white (fluorescent) light increased internode extension up to 400% in *Phaseolus vulgaris*, *Helianthus annuus* and *Ipomea hederacea* (morning glory). When FR was followed by 5 minutes R the effect was fully reversed. Kasperbauer (1971) found the effects of end-of-day FR treatment in tobacco to be similar to the effects of vegetational shade in field conditions. Holmes and Smith (1975, 1977) observed that plants grown in incandescent light showed more stem extension than plants grown under fluorescent light and suggested that this was due to the effect of R:FR ratio. Morgan and Smith (1976) reported that supplementary FR added to background white light led to a stem extension rate that was proportional to the (theoretical) phytochrome equilibrium, at least for the range of photoequilibria found in natural shade.

In order to study the effect of the blue and red wavebands and to reduce the influence of the far-red region Warrington *et al.* (1976) used extremely high irradiances of 60 W/m^2 and 130 W/m^2 on soyabean. The plants under the high irradiance were very compact, whereas the lower irradiance resulted in tall vine-like plants. Those authors depended on Meijer (1971) who reported that high irradiance levels reduced the elongating effects of FR. Their results, though, were not consistent with the measured blue/red ratios, but turned out to be consistent with the R:FR ratios. Rajan *et al.* (1971) observed taller plants and larger leaf area under fluorescent combined with tungsten lamps compared to plants grown under fluorescent tubes alone. He worked with *Gossypium hirsutum*, *Helianthus annuus*, *Phaseolus vulgaris* and *Zea mays*. Thomas and Dunn (1967) found higher dry weight yields in tomatoes under high red, moderate far-red and low blue waveband radiant energy compared to lamps emitting higher blue radiation.

Changes in plant metabolism have been demonstrated to be caused by changes in spectral conditions. Warrington and Mitchell (1976) found that a bias in the visible spectrum influenced the partitioning of assimilates to the various plant parts. Under blue-biased (or high R:FR) light a smaller proportion of photosynthate was utilized to produce leaf area for further assimilation. They observed a close relationship between leaf area and dry matter yield.

Evidence for the promotion of carbohydrate synthesis under red-biased light was presented by Krotkow (1969) and Ogasawara and Miyashi (1970) in *Chlorella* and Szaz and Barsi (1971) in *Vicia faba*. Szaz and Barsi (1971) explain this as additional ATP production in cyclic photophosphorylation, via activation of photosystem I. The same authors and also Voskresenskaja (1972) reported a decrease of fructose and sucrose content under blue-biased light. Voskresenskaja (1972) attributes the regulating role of blue light on the metabolism to the absorption by flavins or carotenoids.

On the other hand, protein concentrations were reported to increase under blue-biased light (Hauschild *et al.*, 1962). Warrington and Mitchell (1976) reported the same for sorghum and, in particular, for soyabeans. Soyabean total amino-acid content was 22% higher under blue-biased (high R:FR) than under red-biased light. The levels of aspartic acid, serine, alanine, and phenylalanine were all increased under blue-biased, but the levels of arginine, glycine, and valine were increased under red-biased light (Raghavan and De Maggio, 1971). Voskresenskaja (1972) reported increases in protein content under blue-biased light in fern gametophytes (*Pteridium aquilinum*). But Warrington and Mitchell (1976) suggest that the changes in protein concentration may be due rather to growth rate changes than to specific wavelengths. They found that on a total leaf basis the protein per total dry weight was in fact higher in red-biased than in blue-biased or high R:FR light.

Influence of Light Quality on Apical Dominance

Field observations have shown that many species branch profusely when growing in the open, but in shade they exhibit complete apical dominance (Kasperbauer, 1971; Tucker

and Mansfield, 1972). In the controlled environment R:FR has had a remarkable control over outgrowth of buds. Five minutes of FR at the end of 8 h photoperiods suppressed branching in tobacco (Kasperbauer, 1971). Irradiation with incandescent light at the end of the daily white light period completely suppressed bud outgrowth in *Xanthium strumarium* (Tucker and Mansfield, 1972). Fluorescent light alone stimulated bud outgrowth in the species. After outgrowth has started, elongation of axillaries is supposed to be promoted by FR (Tucker and Mansfield, 1972).

Morgan and Smith (1981) point out that incandescent light only corresponds to very sparse shade and therefore experiments with more realistic shade light might show greater expression of apical dominance than those observed by some workers who used incandescent light as the sole light source for FR. They also state that no apical dominance was asserted in *Chenopodium album* and *Polygonum persicaria* when grown under high or low fluence rate fluorescent light which might indicate that in natural shade light quantity would not be responsible for suppression of bud outgrowth. But Smith (1982) found that in daytime simulated shade light (low R:FR) lateral bud outgrowth was readily observed in *Chenopodium album* and *Sinapis alba*.

Excision of the youngest leaves did not prevent apical dominance in incandescent light (Tucker and Mansfield, 1972). Morgan and Smith (1981) argue, therefore, that the axillary buds are involved in photoperception for this response. Photoperception by the bud can be observed without difficulty in *Agropyron repens*, where buds break freely in darkness, but are partially suppressed by light (Leakey *et al.*, 1978). Morgan and Smith (1981) pointed out that incandescent light is more effective than fluorescent light in preventing bud outgrowth and that it causes one shoot to assert dominance after bud break.

Growth Substances and Photomorphogenesis

According to Schopfer (1984) light interferes with the realization of genetically determined patterns by selectively stimulating the expression of some parts of the genetic information and inhibiting the expression of others through the catalytic action of enzymes.

This would at least explain the high specificity of photoresponses. But other authors, like Street and Öpik (1984) argue against this idea because some phytochrome controlled events occur within one minute of a light treatment.

There are many observations that light through daylength or phytochrome may change hormone concentrations or balances between hormones or between different forms of the same hormone. But no direct correlations can be made between these changes and morphogenesis. The observed light effects on changes in growth substance concentrations may be the result of conversion between different forms, biosynthesis, transport or the number of binding sites. There are also many indications that phytochrome exerts its effect on membranes and/or membrane associated structures. These alterations may affect the sensitivity of the target tissue to endogenous growth substance action (De Greef and Fredericq, 1983). But, as the same authors state, "It is easy to say that plant development involves a continuous re-routing of metabolic pathways under the influence of environmental and endogenous cues, but it seems very difficult to come to grips with the problem of what these changes are".

E. Leaf Epinasty

Definition and Causes

The term epinasty is used for an increase in the angle subtended by the adaxial surface of a lateral organ and its parent structure (axillary angle) as well as the development of a more downward orientation in plant organs generally. Epinasty is the curvature which results when the adaxial (upper)side of a lateral plant organ grows more rapidly than the abaxial (lower) side. When the abaxial side grows more rapidly the resulting upward curvature of the organ is called hyponasty (Ball, 1969). Epinasty occurs in lateral shoots, petioles and flower parts (Palmer, 1972), although characteristically epinasty takes place in organs with bilateral symmetry. Radially symmetrical organs generally execute tropic movements (Street and Öpik, 1984; Salisbury and Ross, 1985; Kang, 1979).

Epinastic movements are thought to be primarily autonomous, i.e. not induced nor oriented by specific external factors. This separates epinasty from all tropisms which are oriented with respect to external stimuli and from nastic variation movements (Ball, 1969). However, external factors are not totally without effect on epinastic responses. Epinastic curvature can be modified by light, gravity and temperature as well as by some plant pathogens and by water-logging conditions (Kang, 1979; Schlagnhaufer and Arteca, 1985a, 1985b).

The purpose for specific curvature in leaf petioles seems to be to give the leaves an orientation to light which is optimal for the species. When young leaves emerge from the bud their axes appear to lie almost parallel to the shoot axis, but as they grow their petioles elongate and they bend downward to form an angle with the shoot axis until a proper orientation is achieved for photosynthesis.

Physiology of Epinasty

The physiological basis of epinasty is still quite puzzling and probably not even the same in all plants. Palmer (1972) stated that epinasty is a very complex phenomenon because various regions and the various ages of the leaf have varying sensitivities to epinasty-inducing agents, which result in different kinetics for the process. While in young leaves epinasty is induced easily along the entire petiole, in mature, no-longer-growing leaves epinasty shows up only at the extreme base of the petiole.

Influence of gravity

Since plants on biosatellites as well as on clinostats show epinastic curvature of the leaves it is now clear that epinasty is not mainly a reaction to gravity, but is primarily controlled by internal factors (Lyon, 1963; Kang, 1979). Nevertheless, epinasty can be influenced by geotropic stimulation, i.e. hyponasty can be produced in inverted plants, which is an epinastic curvature in the sense of reversed polarization (Ball, 1969). Leike and von Guttenberg (1962) kept *Coleus blumei* plants with auxin-deficient lateral shoots upside down for three days, then applied IAA to the tips of the shoots and rotated them on a horizontal clinostat. The result was an upward

curving of the lateral shoot instead of the normal epinasty.

Ethylene and auxin

There seems to be nearly a consensus that the growth substances ethylene and auxin are involved in bringing about epinasty (Soekarjo, 1965; Harper and Wain, 1971; Palmer, 1972; Baumgartner and Fondeville, 1980 and 1984; Amrhein and Schneebeck, 1980; Saltveit and Larson, 1981; Beyer *et al.*, 1984; Schlagnhaufer and Arteca, 1985a, 1985b). The authors of recent articles either report that auxin-induced epinasty is reduced when ethylene synthesis is inhibited (Schlagnhaufer and Arteca, 1985a; Amrhein and Schneebeck, 1980) or that epinasty increases when ethylene synthesis is increased by blue or far-red light (Baumgartner and Fondeville, 1980 and 1984) or by reorientation, e.g. flexing of poinsettia leaves (Reid *et al.*, 1981; Saltveit and Larson, 1981).

Only Reid *et al.* (1981) exclude the possibility that ethylene is directly responsible for epinastic curvature. Their reasons are 1) that lack of IAA, produced by the removal of bract blades inhibits epinasty, and 2) that inhibitors specific to ethylene synthesis did not change the epinastic angle. Reid *et al.* (1981) argue that redistribution of auxin, which may be induced by ethylene, is the cause for epinasty. Similar ideas are accepted by Kang (1979), who suggested that gravity has an important influence on epinasty.

Bending of organs is generally believed to be initiated by asymmetrical distribution of auxin, if not in all the tissues on the elongating side of the organ (as was accepted in the classical theories) then at least by asymmetrical auxin distribution within the cells of the epidermis (Mertens and Weiler, 1983). It has been known for a long time that ethylene has a strong influence on auxin-transport (Abeles, 1973; Lyon, 1963). Kang and Burg in 1974 observed that ethylene always moves auxin against the gravitational vector. Therefore, Kang (1979) came up with the hypothesis that auxin induces ethylene production, and ethylene, in turn, acts on the auxin transport to bring about asymmetric distribution of auxin, favoring the adaxial side of a petiole.

Kang (1979) starts out with a gravitropic response, in which, according to Hild and Hertel (1972), auxin asymmetry is due to the asymmetric activity of auxin permeases at the membranes of gravistimulated cells, which leads to asymmetric auxin secretion from the cells. The activity of the auxin permeases would be controlled by the presence of the intracellular statoliths on the lower cell membrane, which perceive the gravistimulus.

But constant gravistimulus is counteracted by time-dependent internal adaptation. It has been observed that lateral organs become insensitive to constant gravistimulation and react only to changes in the direction of the gravity vector (Bennet-Clark *et al.*, 1959; Barström, 1971). This adaption would mean that the pressure of the statoliths decreases and that there would be less activity by the auxin permease in the lower part of the cell membrane. As a consequence an increased symmetry of activity would be established.

Such adaptation could generally be expected to develop when an organ is over-stimulated. As proposed by Hild and Hertel (1972) overstimulation, i.e. increase of a physiological stimulus after the dose-response curve has passed its maximum, leads to a decrease in response and may even reverse direction. According to this concept very strong stimulation should lead to inactivation of the auxin permease at the lower cell membrane and, thus, to auxin transport in the opposite direction, which means against gravity. After some time adaptation would normally set in again and auxin could be transported downward again, which would result in the usual direction of growth in lateral organs. But ethylene is supposed to inhibit this adaptation and, therefore, auxin could still be transported upward. Then the cells on the upper side of the petiole could still enlarge and the leaf would remain epinastically bent.

Gibberellins

Epinastic curvature of petioles is alleviated or slightly reversed by gibberellic acid (Palmer, 1964; Soekarjo, 1965). Palmer and Halsall (1969) proved that in plants pretreated with gibberellins auxin transport was greatly enhanced, whereas ethylene

inhibited it. They, therefore, thought it possible that GA and ethylene act on the same regulatory system. Soekarjo (1965) stated that the GA_3 response might be related to the level of the endogenous compounds inhibiting the activity of IAA-destructing enzyme systems.

Light

Epinasty is also influenced by light. Photoepinasty of leaf blades is a typical high irradiance response and has maxima in the blue and in the far-red portions of the spectrum (Baumgartner and Fondeville, and 1984). Those authors found that in *Sinapis alba* the epinastic movements were rapidly induced by blue and far-red light, whereas in red light there was a latent period before the onset of curving. Those authors attribute the promotional differences to different physiological changes in the leaves under different light qualities. Changes in cell permeability and turgor in the leaves may be involved as primary effects of the high irradiance reaction in the induction of photoepinasty. This would be in accordance with the mechanism of opening and closing of *Mimosa pudica* leaves, which involves turgor changes in the motor apparatus of the leaflets. Baumgartner and Fondeville (1984) point out that, although epinastic photoresponse is more rapidly induced in blue than in red or white light, the quantum requirements for 50% epinastic movement are the same for all three light qualities. This could indicate that fluence rate is more important than light quality.

F. Plagiotropism

The regulations and positioning of lateral organs, shoots and roots, is termed plagiotropism. It involves an epinastic control by the dominant apex tending to force the lateral branches downward and a counter-acting negatively geotropic effect on the branch which tends to position it toward the vertical (Zimmermann and Brown, 1971).

The term 'geotropism', which has been replaced mainly during the last 20 years by 'gravitropism'; is applied to phenomena in which plant parts assume orientations specifically related to the direction of the plumb line. It is a mechanism, starting in the germinating seed, to direct the growth of shoots upwards (negative gravitropism) toward the light and the growth of roots downward toward water and nutrients (positive gravitropism).

Trees and Grasses

It was found in the 1930's by Münch that girdling of trees at the base of the leader, as well as debudding and decapitation caused the lower branches to grow upward in hyponasty (Zimmermann and Brown, 1971). The degree of upwardness decreased with the distance from the apex. Another result of the treatments was the formation of an auxiliary leader which caused the lower branches to grow more downward again. The apical control of plagiotropism has been attributed directly or indirectly to auxin which was produced in the terminal leader, although it is not known how the auxin transported down the main stem can counteract the auxin produced in the tips of the lateral branches.

Branch angle can be modified by manipulating the environment. Hyponasty could be induced in some conifers by application of exogenous gibberellic acid, which enhanced the negatively gravitropic growth of a lateral branch after decapitation of the terminal shoot of *Cupressus arizonica* (Pharis and Kuo, 1977; Pharis *et al.*, 1965). The growth appears to be primarily controlled by endogenous GA's. The quantitative level of GA may determine the form, and this may be modified through the use of growth retardants and GA antagonists or environmental treatments (photoperiod), both of which are known to affect the level of endogenous GA (Pharis and Kuo, 1977). Pharis and Kuo found that the growth retardants AMO-1618 and B995 and the GA antagonist morphactin modified the crown form of tall Cupressaceae species. They stated that "in general, positively geotropic growth of the woody shoot occurs under situations assumed to reduce GA levels, negatively geotropic growth in response to added GA."

The same research group has lately found that gibberellins are also involved in the regulation of negative gravitropic curvature in intact *Avena sativa* (oat) plants. Kaufman *et al.* (1985) reported that just one hour after gravistimulation bottom segment halves retained 22% more labelled precursor GA, 36% more free GA-like metabolites, and 48% more GA-glucosyl conjugate-like metabolites than vertical segments. In contrast the one hour gravistimulated top halves retained slightly less labelled precursor and free, GA-like metabolites, but 21% more GA-glucosyl conjugate-like radioactivity than vertical segments.

Herbaceous Dicotyledons

In herbaceous dicotyledons the evidence for the involvement of growth substances in gravitropic curvature is sketchy. In 1959 Dostal observed that tubers of *Circaea intermedia* treated with GA_3 formed many long negatively geotropic filamentous shoots, whereas control tubers developed horizontal stolons. Finn and Nielsen (1959) treated, among others, the dicotyledonous species ladino clover, birdsfoot trefoil and alfalfa with gibberellins which resulted in an upright, open type of growth with little or no tillering while there was a dense cover in the pots with untreated plants. Stoddard (1960) treated red clover (*Trifolium pratense*) with GA_3 and observed early upright growth opposed to a normal, early prostrate growth. Bendixen and Peterson (1962) found that gibberellin application released the stoloniferous strawberry clover (*Trifolium fragiferum* L.) from its natural light-imposed diatropism. Bendixen and Peterson came to the conclusion that an interrelationship between the auxins and gibberellins influenced the tropistic behaviours, since IAA applied together with GA reduced the reaction time whereas IAA alone did not have any effect on tropism. Upward growth was initiated when Wallenstein and Albert (1963) applied GA_3 to *Proserpina palustris* L., a species which grows prostrate under short days but upright under long days. The prostrate habit was assumed to be due to geotropism, since plants illuminated horizontally turned toward the light, but plants illuminated vertically did not. They concluded from the effect of photoperiod that the response of the species to gravity was mediated by phytochrome. They stated, "the phytochrome system therefore interacts with temperature and

externally applied GA_3 to control leaf shapes, leaf orientation, and the geotropic response of the shoot."

Mechanism of Geotropic Bending

The growth regulating mechanism of geotropic curvature in dicotyledons is not understood (Wilkins, 1984; Salisbury and Ross, 1985; Pickard, 1985). The involvement of growth substances, and GA in particular, is a very contentious subject. Growth substances could be involved in any of the steps in the reaction chain of gravity-dependent orientation of plant organs, in perception, transduction or cellular response. In the perception phase specific organs which receive the gravity stimulus may be destroyed by growth substances. In the transduction phase an asymmetry of hormones, protons or ions may develop, and the distribution may be influenced by growth substances directly or indirectly. In the response phase asymmetrical growth occurs in the asymmetrically stimulated tissues. Even here growth substances might change the response to the stimulus.

Perception phase

In the perception stage the starch statolith theory has been tested in many experiments and substantial evidence for its validity has been found (Wilkins, 1984). In a representative experiment Miles (1981) observed that in a non-photosynthetic *Zea mais* mutant the gravitropic responsiveness was lost after the endosperm was used up and the leaf sheath bases did not contain starch any more. But when the leaf sheath was supplied with sucrose the amyloplast formed again and the shoot responded normally to the gravity stimulus. Moore (1986) found that only the redistribution of amyloplast and nuclei correlated positively with gravicurvature. Wendt and Sievers (1986) found that, after high doses of centrifugation, endoplasmic recticulum cisternae relocated independent from the direction of gravity and that this relocation restituted the polarity in the statocysts which is necessary for graviperception. Clifford and Barclay (1980) argue against the role of amyloplasts, since they found their sedimentation to be slow and irregular and that they the amyloplasts were moving around

in cytoplasmic streaming in dandelion flower stalks.

Transduction phase

The transduction phase is still a mystery, although most authors believe that a hormonal asymmetry develops. The classical Cholodny-Went model of 1926 stated that tropic curvatures were the result of unequal distribution of auxin by lateral movement from the upper to the lower side. This theory has been attacked most vigorously by Digby and Firn (1976, 1979) and by Digby *et al.* (1982) saying that the measured redistribution of auxin has never been observed to be as dramatic as it should be considering that the upper side of a horizontal shoot stops growing completely.

Mertens and Weiler (1983) also found only a 2:1 ratio of IAA in the lower compared to the upper side of gravistimulated maize coleoptiles and no asymmetry of IAA, ABA or GA's in gravistimulated hypocotyls of *Helianthus annuus*. But they arrived at an hypothesis for the mechanisms of IAA involvement anyway, based on the following results of their own and others. First, they found that the bending response lag was the same after unilateral supply of sunflower hypocotyls with IAA as after gravity stimulation. They also found that high IAA concentrations accelerated bending responses. Secondly, they cite Brauner and Hager (1958), who reported that auxin depleted tissue of sunflower hypocotyls required the addition of IAA for bending. (This point was made recently also by Hatfield and LaMotte (1984) for maize coleoptiles). Thirdly, Mertens and Weiler go back to the findings of Mentze *et al.* (1977) that auxin-enhanced and acid- enhanced growth was controlled by the epidermis which keeps the inner tissues under tension (also Salisbury and Ross, 1984) and by Mulkey *et al.* (1981) that proton efflux at the lower side of the hypocotyl was increased prior to curving, while gravitropic bending was inhibited by neutral buffers (Wright and Rayle, 1982). Mertens and Weiler argue that the amount of exogenous IAA which has to enter the tissue to enhance the residual gravitropic response is so small that it does not detectably increase the average IAA level in the tissue.Because the amount of IAA already present in the tissue is quite large and consists (probably in all

shoots) of a large, presumably inactive, and a small, potentially active pool. Gravity would induce the release of IAA into the active pool of those cells which have the correct orientation in the gravity field. The active IAA would stimulate proton-extrusion and thereby increase cell wall extensibility and initiate graviresponse.

Involvement of gibberellins in geotropic curvature

The involvement of gibberellins in geotropic bending is even less understood because the role of gibberellins in stem elongation is unclear. GA_3 treatments increased elongation of *Cucumis sativus* hypocotyls (Cleland *et al.*, 1968), *Lactuca sativa* hypocotyls (Stuart and Jones, 1978) as well as *Avena* stem segments (Adams *et al.*, 1975), but only in Avena was an increase in wall extensibility and release of protons into the incubation medium observed (Hebard *et al.*, 1976). In cucumber hypocotyls Cleland found that GA_3 treatment resulted in more than a 5-fold increase in growth, but not in an increase in wall extensibility. Therefore the acid growth theory would not be applicable and Cleland speculates that GA_3 rather causes an increase in hydrolytic and proteolytic enzymes which then cause an increase of osmotic concentrations in cells. Stuart and Jones (1978) found that lettuce hypocotyls in a medium of pH 4.25 reached only 10% of the increase in elongation caused by GA_3, and that hypocotyls treated with GA_3 did not acidify their incubation media, i.e. did not release protons. But nevertheless extensibility of cell walls was increased by GA_3 treatment as well as by darkness. Kawamura *et al.* (1976) reported that GA_3 stimulated lettuce hypocotyl elongation by biochemically modifying the mechanical properties of the cell wall. It caused a substantial increase in cellulose and hemicellulose content per hypocotyl, but their content per unit length of cell wall decreased. Therefore, those authors thought that the ability of the wall to extend increased.

Other authors suggest that gibberellins act indirectly by influencing transport or synthesis of auxins (Okubo and Uemoto, 1985). They report an increase in free gibberellin and diffusible auxin in elongating tulip stems after dark treatment. At the same time bound-form gibberellins decreased. Dark induced elongation was inhibited

by decapitation, although the free gibberellin increased. Okubo and Uemoto conclude that dark induced elongation is promoted by auxin, which is transported from the upper organs due to stimulation from the dark-induced increase in free-form gibberellin. The same authors do not exclude the possibilty that at the same time the gibberellin may also increase auxin synthesis in the elongating internode.

Model of GA-involvement in gravitropism

The only model for GA-involvement in gravitropism comes from Kaufman and Dayanandan (1985) in grass pulvini. They hypothesize that the starch statoliths, when falling to the bottom of the statenchyma, are surrounded by the tonoplast membrane. Thus, any enzyme associated with the starch statoliths may be involved in releasing hormones, such as GA's or IAA from their conjugates. GA conjugates are known to be stored in vacuoles, from which they could be released since the falling starch statoliths may act as vehicles to bring enzymes to the substrate compartments. This could lead to the release of free, active hormones from presumably inactive conjugates. A similar process may occur in dicotyledons.

IV. Research: Strength of Growth Retardant Solutions

A. Introduction

The objective of this experiment was to establish the suitable concentration of the growth retardants chlormequat and ancymidol for the production of compact *Begonia lucerna* under a fairly low irradiance of mixed light from fluorescent and incandescent lamps in growth chambers with 16 and 9 hours of daylight.

Light

Tubular fluorescent lamps are mainly used in phytotrons and multiple-layer cultures. These lamps can be mounted close to the plants because of their large luminous surfaces and low wall temperatures. According to Vince-Prue and Canham (1983) white fluorescent lamps are the best to use when plants are raised entirely under artificial light because they have a broad spectrum. They have a very high output in the blue (400 to 450 nm) and green and yellow (500 to 600 nm) area, but a very low portion in the far-red (over 700 nm) area. Many LD plants do not initiate flowers or do so slowly under fluorescent lights because of their low far-red content (Vince-Prue and Canham, 1983, Nilsen *et al.*, 1979, Holmes and McCartney, 1976). Therefore the addition of incandescent lamps is often recommended to increase FR and R, and thereby change the $P_{fr}:P_{tot}$ ratio. It is suggested that the fluorescent/incandescent ratio should be 9:1 in illuminance or 7:3 in installed lamp wattage (Downs and Hellmers, 1975). But other authors doubt that this ratio is particularly suitable for plant growth in general. Some species, e.g. tomatoes, may develop more elongated stems under fluorescent lamps alone than in a glasshouse.

A relatively low irradiance was used in this experiment because such low light conditions are employed in Europe in the production of the numerous *Begonia* species which are grown there. Commonly in Europe a thick tarpaulin spans across the whole greenhouse at a height of about two meters. According to Kaufman *et al.* (1983) 5400 lx of unspecified light for 12 hours per day should be sufficient for begonia production.

Preliminary Experiments

In preliminary experiments it had been established, that chlormequat and ancymidol effectively inhibit elongation of internodes in *Begonia lucerna* (Appendix 1) and that all axillary buds on the main stem could be expected to develop into branches when the stem was pinched above the second or third visible node (Appendix 2). Pinched *Begonia lucerna* plants grown in a greenhouse with 16 h supplemental incandescent light and treated with various rates of growth retardants resulted in plants with the following average internode lengths (compared to 4 cm internodes in control plants): Ancymidol at 0.20 mg a.i./pot resulted in 2.47 cm internodes, 0.25 mg a.i./pot in 2.4 cm and chlormequat at 165 mg/pot resulted in 2.65 cm internodes, 212 mg a.i./pot in 2.51 cm (Appendix 3). Four unpinched *Begonia lucerna* plants potted, as horizontally as possible in a heavy basket, kept in a shaded greenhouse and treated with 0.25 mg a.i. ancymidol or 212 mg a.i. chlormequat continued growth in the direction of the slanted stem. In contrast, untreated control plants grew upwards in a negatively gravitropic direction under the same growing conditions (Appendix 4).

B. Materials and Methods

The 58 rooted cuttings of *Begonia lucerna* were potted into 5 inch pots filled with a mix of 50% peat and 50% vermiculite with the following amendments per m^3:

8.5 kg agricultural lime

9.2 kg Nutricote 14-14-14 (slow release fertilizer)

0.04 kg fritted trace elements.

All pots were placed in the phytotron of the Biological Sciences Building in a walk-in growth chamber of 24 °C under 55% saran shade resulting in 4500 lx (12.8 W/m^2), composed of 3240 lx (9.5 W/m^2) fluorescent and 810 lx (3.2 W/m^2) incandescent light. Daylength was kept at 16 hours. The saran shade did not alter the light quality. The light was measured in lx (illuminance) at plant height and then converted into W/m^2 (irradiance) according to Thimijan and Heins (1983) to make it comparable to data in the literature. The irradiances in the red band (655 to 665 nm) and in the far-red band (725 to 735 nm) were measured in

$\mu W/m^2/nm$ in order to calculate the R:FR ratio (Table 1).

The pots were kept in trays filled with vermiculite and watered by hand three times per week. All plants were pinched 5 weeks after potting to two, if short internodes and strong buds were present to three, nodes above soil level. Seven weeks after potting the pots were treated with the soil drenches of ancymidol or chlormequat, respectively (Table 2).

Exp. A. After treatment with growth retardants seven pots of each treatment were kept in the same walk-in growth chamber under the same conditions as before.

Exp. B. Three pots each of treatments A-2, C-3, and Control were placed in a growth cabinet in the AgFor Centre under 24 °C and 9 hours of 9300 lx (22.8 W/m^2); 7750 lx (18.8 W/m^2) originating from fluorescent cool white tubes, the remainder from incandescent bulbs. The totally randomized experiment was repeated once. The pots were re-randomized weekly.

C. Results

Notes were taken 14 weeks after potting. The number of flowers and number of internodes developed after pinching were counted, the internode lengths were measured and the general appearance as a potted plant was noted.

Experiment A: Long Days

In the walk-in growth chamber under 16 h days the stems of the control plants were quite weak and would sag down without staking, while the stems of all plants treated with growth retardants were strong, although often horizontal in growth. It was impossible to stake the stems of ancymidol or chlormequat treated plants because they would break rather than bend. The sideways growth did not enhance the appearance of the plants in all three chlormequat treatments (C-1 to C-3) and in the lowest ancymidol treatment (A-1). The shoots were long (Table 3) and the plants were so wide that shipping would create problems. The plants in treatment A-2 and A-3, had strong horizontal growth, but still were of a manageable size because the internodes were short (Table 3). The cane growing from the

lowest bud on the main stem, which was buried below the soil during potting, always showed the strongest horizontal growth. The direction of this branch was always opposite to that of the main stem. All leaves were large and had an excellent green colour with prominent silvery dots. Flowering was excellent in all plants treated with growth retardants.

Control plants did not exhibit any strong horizontal growth, although they were quite open and wide. The long internodes and long stems caused widths of over 50 cm in spite of the normal angle of the shoots. Later these shoots toppled over (Figure 1)

Treatment C- 1 made 3 out of 7 plants grow strongly horizontally (about 55° deviation from the plumb-line). The relatively long internodes enhanced that appearance, particularly when the plants were older. Shoots which were shaded strongly by other plants grew upward, producing a very long internode in the shaded area (Figure 2).

Treatment C-2 caused about the same type of growth as C-1, but the higher canes which grew at a 45° angle balanced the appearance better, although the plants were still too open and wide.

Treatment C-3 resulted in some plants in which all shoots, including those originating from the root area, grew very strongly horizontally (65° deviation from plumb-line) (Figure 3). Other plants had more upright shoots and slightly longer internodes which made the plant look very open. Flowering was very good in this treatment.

Treatment A-1 caused the same problems as the chlormequat treatments. Strong sideways growth (45°) combined with long internodes created a wide and open appearance (Figure 4).

Treatment A-2 resulted in the most attractive plants. In spite of the horizontal growth (60° and more) in all plants the short internodes and abundant flowers created a very compact, healthy appearance. The only draw-back was the asymmetry in some plants (Figure 5), which was alleviated later when the shoot from the lowest bud grew longer.

Treatment A-3 plants were also attractive, but the leaves in some of them looked crowded and the lateral growth in some plants turned into downward growth (Figure 6).

Experiment B: Short Days

In the growth cabinet with 9 h daylight the results were very different. Flowering was much reduced compared to 16 h daylight. Chlormequat had hardly any effect compared to control plants, whereas ancymidol had a very strong effect on internode length (Table 4). The plants treated with ancymidol bent just slightly forward.

Control plants had very weak stems and did not stand up on their own. Internodes were very long (Table 4), flowering was poor, and some leaves abscised (Figure 7).

Treatment A-2: All plants had extremely short internodes (Table 4) and restored apical dominance. The uppermost, dominant shoots bent slightly forward. Leaves showed e[illegible]ty and were small. Only one plant developed a flower cluster, but that occurred directly on the main stem, not on a branch. Two plants of three were quite attractive and saleable (Figure 7) because of their shape.

Treatment C-3: This treatment showed little internode reduction (Table 4). Some stems sagged. Leaves were very large and had good color except one very low leaf on one replicate. The plants developed few flowers and were not saleable (Figure 8).

D. Discussion

Experiment A: Long Days

Light requirement

Begonia lucerna developed quite well under the Saran shade, despite the low irradiance. Vince-Prue and Canham (1983) state that usually plants (which are not further specified) need 30-60 W/m² for 12 hours for satisfactory photosynthesis. If this were distributed over 16 hours 22.5 to 45 W/m² would be needed for satisfactory growth. However there is a great variation between sun plants and shade plants, and even between plants of the same species grown under different conditions in the requirement for photosynthetically active radiation.

Since *Begonia lucerna* is a species which was produced by a plant breeder it does not have a native habitat in which it developed its characteristics for best survival. But the fact that it has survived since circa 1892 (Thompson and Thompson, 1981), in the old and in the new world, mostly being propagated vegetatively, indicates that it must be able to grow under various environments. It is accepted that sun plants are not able to adapt well to lower light, while many woodland plants which grow naturally under a higher canopy are able to grow under varied conditions (Smith and Morgan, 1983). *Begonia lucerna* reacted like a woodland plant, and this should explain why it grows well in different environments, since such plants are on one hand able to photosynthesize under low photosynthetically active radiation and on the other hand are able to outgrow the deeper shade of other plants below the higher canopy. Kaufman *et al.* (1983) rate begonias generally as high light requiring house plants which need about 5400 lx of unspecified light for 12 hours/day, mentioning that flowering types may need more. If this light were distributed over 16 hours the light requirement would be 4050 lx, exactly the illuminance which was supplied to these plants. This light also appeared to be similar to the conditions seen in Wageningen (Netherlands) and Geisenheim (Germany) where begonias are grown in summer under thick grey linen tarpaulins, although no cane-like species are produced there. Cane-like begonias can usually stand more light and even some sun according to Thompson and Thompson (1981).

Control plants grown under this low light without growth retardants were not of marketable quality because the stems were too weak at the bottom to hold their weight. They fell over without breaking after about 10 weeks of growing. The shoots always bent at the bottom of a long internode, whether they were originating from the root area or from a lower node of the original stem. This is a symptom of too low light intensity, where carbohydrate synthesis is somewhat low (Joiner, 1983). Probably the plants shaded each other at the base of the stems and made the first internodes grow longer and weaker because of a low R:FR ratio (Björkman, 1981; Smith, 1982).

The shoots from the root area did not grow up as straight canes under this low light, but grew out at about the same angle as the shoots growing from the main stem. These shoots did not grow more vigorously than the other stems, which is unusual in cane-like begonias. Leaves were large in all treatments which is common under low light (Smith 1982). Leaf size was slightly smaller in the ancymidol-treated plants, particularly in the shoots from the root area. The latter is in keeping with the usual growth pattern of cane-like begonias.

Effects common to ancymidol and chlormequat

In the plants treated with growth retardants the stems were shortened enough to hold their own weight, whether they grew strongly horizontally or in a normal negatively geotropic direction. If the horizontally growing shoots reached an area of deep shade they would grow upward (Figure 2). As long as the plant grows in the direction of a stimulus of higher light this has to be a phototropic response.

But horizontal growth of the lateral shoots generally in an evenly lit room where the light source is above the plants could not be phototropic. It could be a geotropic response, however. As Blake *et al.* (1980) point out decapitation, gibberellic acid, high light and their combination induce branch hyponasty in conifers. Application of growth retardants, on the other hand, resulted in positively geotropic growth of lateral branches under short photoperiods, and this response was prevented by simultaneous GA_3 application (Pharis *et al.*, 1965). Pharis and Kuo (1977) state, therefore, that the direction of branches is primarily controlled by endogenous gibberellins and could be modified by growth retardants. In *Begonia lucerna* the direction of the outgrowing branches in decapitated plants seems to be controlled in a similar way by GA_3 and light level. Since the internodes in plants under lower light were longer than under higher light (chap. V) this may indicate a higher level of GA_3-activity under low light. If there was such higher activity, GA_3 did not prevent the positively gravitropic response. Therefore, Wallenstein and Albert (1963) are probably right in their opinion that the response of plants to gravity appears also mediated by phytochrome, which then

interacts with gibberellins.

Flowering was promoted by both growth substances under long days, as had been found in many species. Miranda and Carlson (1980) and Jansen (1973) concluded that the light requirement for flower induction after treatment with growth retardants was reduced in geranium. The flowers were well visible in the plants treated with growth retardants. The clusters hung down from the nearly horizontal shoots with no interference from lower branches or leaves. For the same reason the flower clusters were particularly large. No leaves were in the way to break or inhibit the single flowers or their pedicels. This is very important in *Begonia lucerna* since the cymose clusters become larger over time, each pedicel giving rise to two new flowers. Some clusters had nine 'generations' of single flowers. From the second or third 'generation' on only female flowers developed. That increased the size of the clusters because the three wings, typical of the female begonia flower, are very large in this species.

Effect of ancymidol

In the ancymidol treated plants internode length in main stem branches decreased with increasing concentration of ancymidol (Table 3). The rate of decrease was 8.6 cm/mg/pot ($Y = -8.59X + 5.1$; $r = -0.99$). On the data for cane internodes analysis of variance was not done since not all plants developed canes. However, when means of the three ancymidol treatments were subjected to linear regression, the correlation coefficient was significant at the 0.01 level ($Y = -17.6X + 7.8$; $r = -0.99$). Only the data for internode length were entered in a statistical analysis because inhibition of internode elongation was the reason for the application of growth retardants. Number of internodes on single shoots or canes and number of flowers per shoot were reported in the table to give an indication to growers what shape of plant to expect after pinching and treatment with growth retardants.

The shorter the internode the stronger the diageotropic growth seemed to be. Even the shoots from the root area grew horizontally and had only slightly longer internodes than the shoots growing out from the original stem (Table 3). This is very

uncommon in cane-like begonias. The reason could be that under the low light intensity under long days the rate of photosynthesis was so low that the plants did not produce enough carbohydrates for more elongation (Vince-Prue and Canham, 1983). Secondly, the gibberellin activity is relatively low under low light (Blake *et al.*, 1980) and could be counteracted easily by a potent growth retardant like ancymidol. Thirdly, it is known that horizontally growing shoots elongate less than upright ones (Palmer, 1964), although this phenomenon is not understood.

Effect of chlormequat

Over the range of concentrations used internode length of main stem branches decreased by 0.07 mm/mg a.i. chlormequat/pot ($Y = -0.007X + 5.05$; $r = -0.99$). Since not all chlormequat treated plants developed canes within the period of observation no analysis of variance was possible and no clear trends were evident in canes.

Internode elongation was inhibited more strongly by ancymidol than by chlormequat, although the amounts used in this experiment had produced similar internode lengths among treatments in the greenhouse (Appendix 3). The reason for the weaker action of chlormequat was probably the higher temperature in this experiment. Heide (1969) had found that chlormequat did not control growth in *Begonia cheimantha* at 24 °C. Bachthaler and Jansen (1985) also observed that temperature had a greater effect than chlormequat on the growth of chrysanthemum. Other authors, like Krauskopf and Nelson (1976), who attributed the weaker effect of chlormequat on begonias in summer compared to plants grown in winter to higher light intensities, probably neglected to consider the influence of higher temperature. The numerous reports of little or no effect of chlormequat observed in Egypt point in the same direction (e.g. Hamza and Helaly, 1983).

Internode length in chlormequat-treated plants decreased with increasing chlormequat strength only in the branches originating from the original stem, but the differences were very small (statistical analysis above), particularly between treatments C-1 and C-2. The reason for the relatively long internodes in treatment C-2 could be that

no plant showed any strongly horizontal growth. All shoots grew at angles of about 45 ° which does not seem to be horizontal enough to reduce the internode length more than the normal reduction by the growth retardant. In treatment C-1 and C-3 some plants had horizontal shoots with shorter internodes than the more upright growing ones, which reduced the average length of internodes somewhat in these treatments. Again, there was no difference between the angle of the shoots from the main stem and the shoots from the root area (55° and 65°), which could indicate phytochrome involvement (Wallenstein and Albert, 1963) in a geotropic response, since chlormequat was obviously not strongly inhibiting GA_3 synthesis or transport in these plants. The length of the internodes on the canes from the root area were relatively short, probably because of the low rate of photosynthesis under the low light intensity. The length did not decrease with the increase in chlormequat concentration; rather the length was greatest in C-2 with the relatively upright growth of 45 ° in all plants of this treatment.

Experiment B: Short Days

Plants grown under 9 h days differed markedly from those under 16 h days, although temperature and total daily irradiance (from the same light sources) were equal.

Flowering

Flowering was inhibited under 9 h light. While all plants flowered well under 16 h light in Expt. A (Table 3), only 33% of the plants under 9 h had any flowers (Table 4). This shows that *Begonia lucerna* is not a short day plant, unlike some of the Elatior begonias, and that they require long days to flower well. The temperature of 24 °C usually had a flower-promoting effect, but the short photoperiod must have overridden that effect.

Vegetative growth

Internode length in the control plants under 9 h days (Table 4) was about the same as in control plants under 16 h of low irradiation (Table 3). This is in contrast to

Jungbauer (1980) who reported shortening of stems in Eliator begonia under short days (10 h) and also in contrast to Salisbury (1981) who agrees with Garner and Allard (1923) that stem elongation in response to long days is probably the most widespread photoperiodic phenomenon. Salisbury and Ross (1984) also show tomato plants grown under 16 h light with stems twice as long as plants grown under 8 h light. But photoperiod responses are highly specific and there are at least two reports by Heins *et al.* (1982a) and by Wilkins *et al.* (1986) that shorter light durations caused longer internodes, in Easter lily. Therefore, there is a possibility that the long internodes in the control plants and in the chlormequat treated plants were caused by photoperiodism.

It is more probable, though, that the relatively long internodes are a photomorphogenic reaction to the shade produced by the plants in the small growth cabinet. Vegetational shade is known to have a high proportion of FR and therefore promotes elongation of the internodes. All the light in the growth chamber came from the ceiling and the foliage of the closely spaced plants shaded their own lower internodes. The internode which perceives the shade also reacts to it (Gaba and Black, 1983) with elongation. Probably GA is involved in this process because elongation is reduced by growth retardants, like ancymidol and chlormequat which are known to inhibit synthesis of gibberellic acid.

Since under shade, photosynthesis is reduced whereas photomorphogenic elongation is stimulated, the quality of the elongating stems suffers (Heins *et al.*, 1982b). They are weak and topple over. Carbohydrate synthesis is probably so low that no carbohydrates are stored, plants become leggy, sometimes with light green foliage, weak stems and essentially no flowering (Joiner *et al.*, 1983).

In the short day experiment, analysis of variance revealed significant effect of ancymidol on main stem internode length. In contrast, chlormequat did not reduce internode length compared to control. There was also no significant difference between the internode length in the canes of the chlormequat treated and control plants, whereas a significant difference (.05 level) between the ancymidol-treated plants and the control

was evident.

Effect of ancymidol

The epinastic leaves in the ancymidol treated plants mirror the results of *Begonia lucerna* grown under daylight (January to March) supplemented with incandescent light to prolong the photoperiod to 16 h (Figure 9). In preliminary experiments (Appendix 1) epinasty was observed in control plants as well as in ancymidol or chlormequat treated plants, as long as they were placed directly under the lamps. Since the plants in both experiments in which leaf epinasty occurred were bending over only slightly, gravity probably was not involved in this response. The treatment with obviously efficient growth substances which are known to inhibit gibberellic acid synthesis could play a part, since Palmer and Halsall (1969) and Soekarjo (1965) found that gibberellins probably had an indirect influence, through auxin transport regulation, on epinastic curving of petioles.

Light quality, i.e. high FR content, probably had a great effect on the epinasty in Expt. B, since the phenomenon was only observed under vegetational shade. Leaf epinasty also had occurred before under 16 h incandescent supplemental light in a greenhouse (Appendix 1). These are two situations where FR content is known to be high (Anon. 1982). Epinasty was not observed in the experiments under mixed light when the R:FR ratio was 1.4 (Table 1), which indicates low FR content. At that ratio it did not matter whether the light intensity was low, i.e. under shade mesh (Expt. A, chap. IV), or higher, i.e. without the shade mesh (Expt. in growth chamber, chap. V). Furthermore, epinasty did not occur in the greenhouse in winter when HPS-light was used to supplement daylight (Expt. in greenhouse, chap. V). It is known that HPS-light contains little FR (Anon. 1982).

On the other hand, in the experiment reported in Appendix 1 the FR in the incandescent light (16 h) had a great effect. Since daylight lasts only for about 9 hours in our area in winter these plants were exposed to 7 h of only incandescent light. The photoperiodic incandescent lighting provided enough irradiation for the

photomorphogenic effect (Vince-Prue and Canham, 1983). These results seem to indicate that light quality plays a role in epinastic bending of green petioles after all, although it has been stated that fluence rate is more important in green tissue (Baumgartner and Fondeville, 1984).

Ancymidol reduced internode length more under the short photoperiod in Expt. B than under the low light intensity under long days (Expt. A), although the total daily irradiance was the same as in Expt. B (204.8 W/m^2 per day under long days compared to 205.2 W/m^2 per day under short days). The outgrowing branches had only a few internodes. The lower shoots which sometimes appeared rudimentary indicate that indeed the high FR radiation had a similar influence on the growth as reported by Kasperbauer (1971) for tobacco. Under the dense canopy of the higher growing plants the growth of the axillary shoots was inhibited, whereas the highest shoot developed quickly in an effort to outgrow the canopy (Tucker and Mansfield, 1972). This quick development resulted in formation of nodes at the same rate on the highest shoot as in the untreated plants. Internode elongation was inhibited, though, by ancymidol because gibberellic acid is involved somewhere in the process of elongation caused by high FR or low R:FR ratio (Lockhart, 1956; de Greef and Fredericq, 1983). The biosynthesis or the action of gibberellic acid was probably inhibited by ancymidol. In accordance with Krauskopf and Nelson (1976) ancymidol was found to be effective under high and low light. But according to the same authors ancymidol is more effective under low light. This could explain the extreme shortness of the youngest internodes in the sideshoots of the ancymidol treated plants, which were growing in the shade of the untreated or only weakly reacting plants.

Effect of chlormequat

Chlormequat, on the other hand, probably had no effect under SD because it interacts strongly with environmental conditions. Krauskopf and Nelson (1976) found 0.3% drenches ineffective when applied in early October, but excessive when applied to a winter grown crop of Elatior begonias in North Carolina. Heide (1969) reports much

higher efficiency of chlormequat under low temperature than under high temperature, where even growth stimulation occurred under high light.

The lack of or very weak action of chlormequat under 9 h light and 24 °C might be due to the closeness of the plants in the growth cabinet. The lower and middle internodes were especially long in these plants because they were shaded and the high FR content led to elongation through the involvement of gibberellic acid. The plants probably also had a very high auxin (or gibberellin) content since they had been held in a 24 °C growth chamber with 16 h daylight after pinching and up to the chlormequat treatment. They were growing vigorously at the time of treatment. The status of growth hormones in the plants seems to be of particular significance on the effect of later applied chlormequat. Not only Krauskopf and Nelson (1976) report the inefficiency of later applied substance on begonias grown under the high light intensity of August and September, but also Wilfret (1984) reports its inefficiency on poinsettas treated before the end of September in Florida. Heide (1969) mentions the possibility that the high auxin level of begonias grown at high temperatures may be one reason for the reduced effect of chlormequat.

Another concomitant reason could be that the non-reacting plants were reaching the ceiling of the growth cabinet and were thereby very close to the hot incandescent lamps. The heat of these lamps was ventilated out of the cabinet, but with the lamps so close to the plants the heat must have had an influence on the highest shoots. Another effect of the closeness of the lamps may have been that the tips of some plants grew closer to incandescent bulbs than to fluorescent fixtures. Thereby they would receive a great proportion of FR which again would promote elongation of the internodes.

E. Conclusion

Overall it can be concluded that ancymidol treatments, and especially the A-2 treatment with 0.25 mg (a.i.) ancymidol per pot resulted in attractive plants of fairly even size and shape. The use of ancymidol can be recommended for the production of *Begonia lucerna* as potted plants, under the conditions described.

Chlormequat, on the other hand, cannot be recommended for the production of *Begonia lucerna*. Its effectiveness is hampered too much by the relatively high temperature needed to shorten production time. Within the treatments used the plants were too diverse for selling in size and especially in shape. Some grew upward and some horizontally under the relatively low light intensities which are common in begonia production. But chlormequat had some effect on *Begonia lucerna* and since it is so economical growers are encouraged to try it under their own growing conditions.

Another important conclusion to be drawn from Experiment B is that *Begonia lucerna*, unlike some Rieger Elatior begonias, is a long day plant and needs more than 9 hours of daylight for acceptable flowering.

An abstract of the results in this chapter was published in HortScience in 1984 (Marahrens and Toop, 1984).

V. Research: Fertilizer, Temperature and Light

A. Introduction

This experiment was carried out to study the influence of different fertilizers on the development of *Begonia lucerna*. The same walk-in growth chamber with the same high temperature, as in Chapt. IV, Expt. A, and high but unshaded light was used to investigate the possibility of shortening production time. A greenhouse compartment was also used which turned quite cool (to 16 °C) during a cold spell and received supplemental lighting from high pressure sodium lamps. The growing conditions in the two locations are not directly comparable. The greenhouse was used because the conditions are the same as growers can provide. The growth chamber had the advantage that the light intensity could be changed with Saran mesh and that the temperature could be kept high to observe the species' reaction.

Light

High pressure sodium (HPS) lamps (SON-T) combine high radiant efficiency (253 mW/W) with a spectral distribution that is suitable for a wide variety of crops. The highest output occurs in the 550 to 620 nm range (Anon., 1982), but there is some light emitted as a continuum throughout the visible spectrum, including also FR. For some species HPS-lamps do not emit enough blue for satisfactory growth and flowering when they are used as the sole light source (Cathey and Campbell, 1975). But HPS-lamps are highly recommended and widely used as a supplementary light source for daylight in winter. The Philips Company recommends 7000 to 9000 mW/m² supplemental light from high intensity discharge lamps in winter for improving vegetative growth in Rieger, Lorraine and Rex begonias (Anon., 1982).

Fertilizers

Begonias are not heavy feeders and fertilizer levels should be kept low (Ball, 1975). Overenriched growing media encourage growth at the cost of flowers. This problem had to be

considered particularly in the case of all experiments with the tall *Begonia lucerna* which was to be kept at a manageable size without showing deficiency symptoms. Most published recommendations for fertilizing Rieger begonias include slow release material and supplemental nutrient solutions for watering (Wikesjö and Schüssler, 1982; Schenk and Brundert, 1980; Nelson *et al.*, 1977, 1978, 1979). Unfortunately, these publications never give the total amount of fertilizers used, but only ratios of N, P_2O_5 and K_2O in the watering solutions. Nelson *et al.* (1978) who researched the nutrient requirements for Rieger begonias in depth state that weekly applications of fertilizer solutions containing 440 ppm N or more and 150 ppm N or less resulted in undesirable plant size reductions. Some European publications (v. Hentig and Knösel, 1981; Reuther, 1980) give specific amounts of commercial fertilizer mixes (like Poly Crescal 14(N)-10(P)-14(K)) which are not available here. The problem with these mixes is that their content of other nutrients is not made public.

Nutricote 14-14-14 was recommended for Rieger begonias by Holcomb (1979) at 1 oz./gallon of medium (6.6 kg/m³). Osmocote 18-9-9 with a 8- to 9-months dissolution rate was recommended by Maynard and Lorenz (1979) at 9 kg/m³ to be incorporated in the mix for Rieger begonias. Superphosphate amendments seem to be very popular in the production of potted plants. They were used by Nelson *et al.* (1978) and recommended by Wikesjö and Schüssler (1982) for Rieger begonias at 12.5 oz./yard³ (384 g/m³) in addition to 12.5 oz./yard³ Osmocote 14-14-14 (480 g/m³), 5.5 oz./yard³ potassium nitrate (210 g/m³), 1 lb/yard³ magnesium sulfate (580 g/m³), and 9.7 lb/yard³ ground limestone (5640 g/m³).

Liquid fertilizer additions alone were tried in this experiment, since many growers supply nutrients with the water, either daily or weekly. A fertilizer with the analysis 15-30-15 was used to establish good fibrous roots in the growing medium after potting and later for flower induction and development. Liquid 20-20-20 was used during the time of vegetative growth after pinching.

Preliminary Experiments

In preliminary experiments the medium containing superphosphate (Appendix 3) (in which good *Begonia semperflorens* as bedding plants were produced) had caused watery spots which developed into necrotic crescents on the leaf margins. These lesions made the plants unsaleable. In order to verify that it was the superphosphate in the growing medium that was responsible for the damage, the 0-20-0 mix (treatment 3) was included in this experiment.

In Nutricote 14-14-14 amended medium *Begonia lucerna* plants developed well in the experiments A and B in chap. IV, as well as in a greenhouse in summer (Appendix 6). Nutricote 14-14-14 was used in this experiment in order to verify that this fertilizer could be recommended to growers for various growing conditions.

Osmocote 18-9-9 amended medium was used to grow *Begonia lucerna* in a greenhouse in summer (Appendix 6). Plants developed without any problems in the medium and showed somewhat longer internodes than those grown in 14-14-14 amended mix.

The medium amended with lime only, but watered in with 20-20-20 solution was also included in the experiment in the greenhouse in summer (Appendix 6). Since this treatment resulted in very short internodes it was decided to apply liquid fertilizer every second week.

All plants used in the experiment reported in Appendix 6 were very compact and full flowering. Since internode length were observed to be relatively long under low light intensity (chap. IV) it was expected that the same strength of ancymidol solution would give a substantial reduction under the higher light intensity in the growth chamber without Saran mesh. The liquid fertilizers were used with (Treatment 4) and without lime amendments (Treatment 5) to the growing media because lime seemed initially to have a beneficial effect on foliar symptoms in former experiments, although pH had turned out to be no problem in the range between 4.5 and 6.5. This is also mentioned in the literature for other *Begonia* species (Schenk and Brundert, 1980; v. Hentig and Knösel, 1981).

B. Materials and Methods

Peat-vermiculite mix (1:1) was used as a growing medium with the following amendments per m^3:

Treatment 1. 9.5 kg Nutricote 14-14-14,
8.5 kg agricultural lime
0.043 kg fritted trace elements.

Treatment 2. 9.5 kg Osmocote 18-9-9
8.5 kg agricultural lime
0.043 kg fritted trace elements

Treatment 3. 2.85 kg agricultural lime
1.25 kg 0-20-0 (superphosphate)
0.60 kg 14-0-44 (potassium nitrate)
0.06 kg fritted trace elements

Treatment 4. 8.5 kg agricultural lime, watered in with 100 mℓ 0.05% 15-30-15 solution, weekly 100 mℓ 0.5% 20-20-20 solutions until ancymidol treatment, weekly 15-30-15 solutions thereafter. (Fertilizer applications in the greenhouse were reduced during a cold spell).

Treatment 5. No soil amendments,
liquid fertilizer supplied as in treatment 4.

In October 1984 ten rooted tip cuttings each were potted in growing medium treatments 1 to 5. Five rooted leaf bud cuttings each were potted in growing medium treatments 1 and 2. Five pots with tip cuttings in each of the 5 treatments were placed in each of the following environments:

a. a growth chamber at 24 °C with 16 h light of 8000 lux (23.5 W/m^2) total, composed of 6400 lux (18.8 W/m^2) from fluorescent and 1600 lux (4.71 W/m^2) from incandescent sources.

b. a greenhouse compartment at 19 °C (± 3 °C) with daylight supplemented with HPS-lamps of 3150 lux (7.7 W/m^2) and an approximate total of 5400 lux

(16.9 W/m²) measured under cloud cover and 17,300 lux (66.5 W/m²) measured on a sunny day.

All pots with leaf bud cuttings were placed in the greenhouse (see b above).

Four weeks after potting all tip cuttings were pinched to 3, and leaf bud cuttings to two nodes above the soil level. Seven weeks after potting all pots were drenched with 0.25 mg a.i. ancymidol per pot. All growth chamber and greenhouse experiments were arranged in a completely randomized design having 5 replicates of 5 treatments. Experiments were re-randomized at weekly intervals. Notes were taken 10 weeks and 14 weeks after potting. A chemical analysis of the leaf tissues was done by Norwest Labs.

C. Results

Differences between Plants in Growth Chamber and Greenhouse

The main differences between the two rooms were 1) the *Begonia lucerna* plants in the 19 °C greenhouse compartment developed more slowly than in the 24 °C growth chamber in spite of the higher light during day time in the greenhouse. (Tables 4 and 5) This was expressed in the greater number of internodes per shoot in the warmer growth chamber in all but the barely surviving plants grown with 18-9-9, 2) the detrimental influences of soil amendments were more strongly expressed at higher temperature and constant light than under lower temperature and variable light intensity. More plants died in treatment 2 and the rest were in much poorer shape in the growth chamber (Tables 4 and 5; Fig. 10) than in the greenhouse. Also more watery spots and papery necroses occurred in the growth chamber in treatment 3 and 5 than in the greenhouse.

Differences between Light Intensities

The shoots on the plants grown without shade did not grow horizontally as did the ones grown under shade. When the internodes of the plants used in this experiment are compared to those grown under 55% shade cloth under otherwise equal conditions (Chap. IV,

Exp. A, treatment A-2) it becomes clear that the internodes under shade mesh are longer, in spite of the fact that the amount of ancymidol solution was kept the same at 0.25 mg a.i. per pot. The internodes of the plants grown in 14-14-14 mix under shade mesh were 2.8 cm, (Table 3) whereas without shade they were 1.8 cm, on the average, (Table 6)

Osmocote 18-9-9

In growth chamber

Osmocote 18-9-9 (Treatment 2) resulted in the death of 3 out of 5 plants in the growth room (Table 5). The roots of the dead plants did not show any newly developed light-colored growth. The survival of the two last plants from the growth room also seemed doubtful for some time. Only one of these could be pinched since the other had not grown at all during the first weeks. The original leaves on the potted cuttings became extremely brittle and yellowish and abscised later, whereas the growing points survived and started to grow after some time. Only the one plant shown in Fig. 10 developed a number of leaves and a relatively great number of flowers. On the other survivor only the original (unpinched) shoot was still growing (4 internodes), while the shoot that had come up from the lowest bud below soil had a dead terminal bud. In both plants the lowest leaves showed some marginal necrosis 90 days after potting (Figures 10 and 16). The plants from the growth chamber did not have any silvery dots at all on the very light green young leaves which were the only surviving leaves. Leaf size was larger in this than in any other treatment. The healthiest survivor had 3 flower clusters, but was not marketable because of its colour and shape.

In greenhouse

The plants grown in the 18-9-9 mix in the greenhouse obviously had been under stress too, since one out of 5 died. Some plants grown from tip cuttings lost the lowest leaf which, again, had become somewhat brittle. The 4 surviving tip-cuttings did not show any signs of problems, even developed better and faster than the tip-cuttings

potted in mix with Nutricote 14-14-14 (Table 6), which was usually the most favorable mix for growing *Begonia lucerna*. Plants grown in the greenhouse had excellent green leaves and prominent silvery dots. No flowers were visible after 10 weeks, but later these plants flowered profusely. These plants could be marketed, even before flowering because of this colour and shape.

Plants grown in 0-20-0 Mix

In growth chamber

The plants in the 0-20-0 mix grew quite well in the growth chamber (Figure 11), but they developed many watery areas of up to 2.5 cm in diameter close to the leaf margins which later turned papery and necrotic. This problem was much more severe in the plants from the growth chamber than in those from the greenhouse. These were the same symptoms which had marred the plants in the early stages of this study.

Not all buds on the original stems developed after pinching, some buds just shed their scales, but did not grow out. This always happened on the second bud from the tip. Some of the badly damaged lower leaves abscised, others showed a pale yellow-brownish discoloration. The internodes on the canes from the root area were long (Table 5) and looked very bare when a leaf was lost. No plant looked full. The internodes which developed first after pinching were long compared to the younger internodes. The leaves from the younger internodes were not able to adequately cover these long stems.

The plants in this treatment flowered less and later than those in the other treatments in the growth chamber. No plant was marketable because of the leaf damage and the shape of the plants.

In greenhouse

The plants grown in this medium in the greenhouse looked stunted. The outgrowing shoots had very short internodes (Table 6) which prevented a full appearance, since every shoot was still visible. The impression of bareness was particularly bad in plants with long internodes on the original, pinched stem, as is shown in Figure 11.

Plants in the greenhouse had somewhat yellowish green leaves on which the silvery dots were very small and faded. The underside of the leaves was brownish red instead of purplish red. The size of the younger leaves was about average. Lesions on the leaves were still few and small after 10 weeks, but increased in number and size later on.

The flower buds started to show color after 12 weeks, i.e. later than in healthy plants in other treatments. Flowering never became as profuse as in healthy plants. These plants were not saleable because of shape and necrotic areas on the leaves.

Plants Grown in Medium Amended with Lime only

In growth chamber

Plants grown in peat-vermiculite mix amended with lime and provided with weekly liquid fertilizer developed great vigour (Figure 12). In the growth-chamber the growth of canes from the root area seemed to be more promoted than in the greenhouse. This was the only treatment in which some plants produced more than one cane per plant after only 10 weeks. In spite of that these canes had a relatively great number of internodes (Table 5), and the internodes were relatively long. In contrast, the branches on the main stems had fewer internodes than the branches on plants in the other treatments. The low number of branches on the main shoots turned out to be due to missing buds. All buds which could grow out did so, although that outgrowth was definitely hampered on plants with more than one shoot growing from the root area. The secondary canes which later came up from adventitious buds below the soil line were very vigorous and had very long internodes. Pinching of these canes to the

second node turned out to be very successful.

The plants from the growth chamber were of a dull green to which the silvery dots did not contrast well. Leaves which had been shaded were light green. There were very few small dry areas on the leaf margins on plants grown in both locations. These spots did not detract from the appearance. All plants grown in the growth chamber had small flower clusters after 10 weeks. They would be somewhat difficult to ship because of their large size. On the other hand, because of their size they would be in a higher price class and also could be harvested earlier.

In greenhouse

The plants in medium amended with lime only but supplied with liquid fertilizer (Treatment 4), and grown in the greenhouse developed excellently (Figure 12). In spite of the fact that the cane from the root area was still in the bud stage and did not contribute anything to the appearances, the plants looked very full, even when two only shoots were present on the original stem. The leaves on the branches started very close to the main stem and grew on short internodes (Table 6), overlapping partly in such a way that there were no uncovered gaps around the plant.

The color of the leaves grown in the greenhouse was very good, the silvery dots large, plentiful and very prominent. The size of the leaves was relatively small, but just right for the size of the plants. Only one plant out of five was flowering after 10 weeks, but all flowered after 12 weeks. Overall, the plants grown in the greenhouse in this treatment after 10 weeks had the best shape for marketing compared to all other treatments. They had the round look and were compact enough for easy shipping.

Plants Grown in Medium without Any Amendment

In growth chamber

The plants without any amendment and supplied with liquid fertilizer (Treatment 5) looked not quite as vigorous, but as full as those grown with lime in the

medium (Figure 13). The plants from the growth chamber were of particularly good shape. The number of shoots per plant and the number of internodes per shoot (Table 5) were slightly higher in these plants than those in the limed medium. The average length of internodes on the branches grown out of the main stems were about the same length as the internodes of the canes. The advantage of these plants was that the internodes of the canes were not as long as those from the lime amended medium (Treatment 4). There were no canes developing from adventitious buds, only the usual outgrowth of the lowest bud on the cutting which was buried in the soil. The leaves of the plants grown in the growth chamber were somewhat yellowish and leaf size was average. Marginal necroses made the plants unsaleable after 10 weeks, although the damage decreased later. All plants from the growth chamber were flowering after 12 weeks, although only one out of five had shown color at ten weeks.

In greenhouse

The plants grown in the greenhouse also had more internodes per shoot than those from the limed medium (Table 6), but the average number of branches on the plants was lower and, more importantly, number and length of internodes were very uneven. Apical dominance seemed to have set in again, making the highest outgrowing shoot become very strong and hamper the development of the lower branches on the main stem. But the shape of these plants was good. As in the plants from the limed medium no shoot (even from the buried buds) had developed yet to make the plants look uneven.

Leaves on the plants from the greenhouse had a good green color, but they had leaf margins with necrotic areas. These necroses were so small that the margins were only indented and the damage was not very visible, but it was present even on the younger leaves. This damage did not occur in later growth. Leaf size was smaller than in the lime amended medium on the plants grown in the greenhouse with the same treatment. None of the plants from the greenhouse was flowering after 10 weeks and only 3 out of 5 were flowering after 12 weeks. Overall, these plants were of saleable

quality in spite of the slight damage on the leaf margins. As in the medium amended with lime the slower growing plants from the greenhouse were more attractive because they had not yet developed any shoots from the root area and because the green was deeper and the silvery dots more visible.

Nutricote 14-14-14

In growth chamber

The plants grown in medium amended with Nutricote 14-14-14 were the healthiest (Figure 14). The plants grown in the growth chamber were very big after 10 weeks. Every bud on the main stem developed into a shoot and the average number of internodes of 4.6 on these shoots developed after ten weeks was by far the highest (Table 5). The average internode length of 1.85 cm was just right for the size. Shorter internodes would have hidden the flower clusters under the leaves. The only problem regarding shape was the very fast growing canes from the lowest bud on the main stem which appeared from below the soil line. These canes had quite long older internodes, which were 7 cm in most plants, and 10 cm in one of them. After these shoots outgrew the upper branches their new internodes became much shorter, but the appearance of the plant was uneven. The leaves on the plants grown in the growth chamber had developed so fast, and a great number of them were still so young that they were still light green with only pale silvery dots. Even on the older leaves the dots were not very prominent. Many leaves had not fully expanded yet, since the plants were growing so fast. Hardly any blemish could be detected on the leaf margins. All plants from the growth chamber were flowering ten weeks after potting, even on some of the shoots from the root area. As mentioned before, the flowers were very visible because the foliage was not too dense. The size of the clusters was excellent from the beginning, by far the largest of all. The Nutricote 14-14-14 mix is very suitable for producing well grown and good flowering *Begonia lucerna*. The plants grown in the growth chamber were ready for sale in record time. They should be taken out of the 24 °C room after

eight weeks at the latest and then kept under lower light and lower temperature to harden off before they are sold. The plants were quite succulent and tall and therefore somewhat difficult to ship, particularly if they have large flower clusters. On the other hand, such plants would bring a good price.

In greenhouse

1. *Tip Cuttings*

The plants grown in the cool greenhouse were smaller because they had developed a smaller number of internodes (Figure 14), whereas the length of the internodes was about the same as for the plants from the growth chamber (Table 6). This was true not only for the internodes on the shoots from the original stem (1.8 cm), but also on the shoots originating below the soil line (3.13 cm). These relatively long internodes made the plants grown in 14-14-14 mix the highest of all plants grown in the greenhouse. They were good plants, but could have profited from slightly more growth retardant or slightly less fertilizer.

The leaves of greenhouse-grown plants looked perfect with their very healthy green and numerous well sized, silvery dots. The large size of these leaves looked attractive on the relatively tall plants and increased the impression of lush healthy growth. Only one of the five greenhouse-grown plants was flowering after 10 weeks, but all of them were at least showing color after 12 weeks (Figures 14 and 15). The plants from the greenhouse were of excellent shape for sale, although they were slightly on the tall side. But the height and, particularly, the height of the cane developing from the root area, i.e. from the lowest bud on the main stem, makes their appearance second best in the greenhouse-grown group. The best ones were those grown in medium amended with lime only and provided with nutrients by liquid fertilizer, mainly because of their symmetrical shape.

2. *Leaf Bud Cuttings*

The leaf bud cuttings grown in 18-9-9 mix (Figure 16) developed 3.0 internodes/shoot within 10 weeks after potting compared to 2.4 internodes/shoot on the plants in

14-14-14 (Figure 15). There was no significant difference between the lengths of internodes on the branches of the main stem on the plants grown in 14-14-14 and the plants grown with 18-9-9 (Tables 7 and 6). No statistical analysis on the internodes of canes growing from below the soil line was possible since not all plants developed canes. However, two out of five 18-9-9 plants developed more than one cane from the root area. Leaf colour was deep green with prominent silvery dots, which made them marketable as small plants even before flowering after 10 weeks. The shape of the plants grown from leaf bud cuttings was excellent, full and round.

Rating

The final rating (1 to 5) of the plants grown in the five different treatments is given below. They are separated into 2 groups according to location because of their size, since it is difficult to compare plants of such differing heights and widths. A rating of 1 is most desirable and 5 the least desirable.

In growth chamber under 23 W/m^2 at 24 °C	In greenhouse under variable light at 19 °C
1) Treatment 1 (with 14-14-14)	1) Treatment 4 (with lime only)
2) Treatment 4 (with lime only)	2) Treatment 1 (with 14-14-14)
3) Treatment 5 (no amendment)	3) Treatment 2 (with 18-9-9)
4) Treatment 3 (with 0-20-0)	4) Treatment 5 (no amendments)
5) Treatment 2 (with 18-9-9)	5) Treatment 3 (with 0-20-0)

This rating is mainly based on marketability and survival. No plants grown with 0-20-0 could be sold. But the low survival rate in the growth chamber in medium with 18-9-9 resulted in the lowest rating for this amendment. In spite of the death of one plant in the 18-9-9 treatment in the greenhouse, two other media were rated lower because of damage on the leaves in both treatments and the extreme openness of the plants grown with 0-20-0 (Treatment 3).

Summary of Results

Light

The most important general result from the experiments was that light had a great influence on the development of *Begonia lucerna* plants, treated with growth retardants. Firstly, very low light was sufficient for their development, 12.7 W/m² under shade cloth (Expt. A, chap. IV), although they grew well also under the same conditions without shade mesh (23.5 W/m²) (chap. V, in growth chamber) and in a greenhouse under supplemental HPS-light (17.3 to 66.5 W/m²). Secondly, under shade mesh (Expt. A, chap. IV) the new growth after pinching and treatment with ancymidol or chlormequat had a very prominent horizontal direction which was not the case under the unshaded lights (chap. V, in growth chamber) under natural light in summer (Appendix 6) nor under natural light supplemented by high pressure sodium light in winter (chap. V, in greenhouse). Thirdly, internode length was longer under 55% shade cloth than under the same lights unshaded, and under daylight or supplemented daylight. Fourthly, internode length was shortened very strongly by ancymidol when the elongation was due to shading of the internodes, as was shown by the results from the growth cabinet experiment (Expt. B, chap. IV). Fifthly, *Begonia lucerna* did not flower under 9 h days.

Fertilizer

The problems encountered during the early experiments, the watery spots on the leaves which dried into papery necroses were diagnosed by tissue analysis to be a boron toxicity and were definitely caused by the fertilizer in the growing medium because the symptoms mainly showed up in the plants grown in the 0-20-0 mix. The plants grown in the unamended peat-vermiculite mix showed small lesions very close to the leaf margins only. It is possible that some excess boron may have remained in some of the plants grown on in media without 0-20-0 since boron accumulates in the tissues. It could be present in the cuttings taken from motherplants produced in 0-20-0 mix.

Since the damage shows up only in older leaves cuttings may look healthy but develop the symptoms later.

D. Discussion

0-20-0 Mix

The fact that the plants in the warm growth chamber developed many more necrotic crescents on the leaf margins than those in the cool greenhouse supports the premise that the problem was caused by the fertilizer which is more readily available to plants under higher temperatures. Since the problem seemed to be related to the use of superphosphate which is known to cause fluoride toxicity symptoms in sensitive species because of its 1 to 4% content of fluorides (Joiner, 1983; Conover and Poole, 1982), it was first suspected that the symptoms were caused by too much fluoride. But tissue analyses showed the same or even higher F content in healthy as compared to damaged leaves, i.e. 98 ppm in healthy control leaves, 48 to 64 ppm in leaves with necroses and 112 ppm in leaves where the damaged tissue was still watery. Therefore, it appears unlikely that the symptoms were caused by fluoride.

Further tissue analyses showed very high boron content (375 and 320 ppm) in leaves with necrotic crescents grown with 0-20-0, whereas leaves which still showed watery leaf symptoms contained only 81 ppm, essentially the same as the 83 ppm found in undamaged tissues in an earlier analysis. It is possible that the washing of the leaves with watery symptoms removed some boron before the analysis was done. Marousky (1981) reported that some symptoms of leaf injury caused by fluorides and by boron are similar, particularly in the early stages, yet distinguishable nevertheless by chlorotic and necrotic base leaves present in plants with too much fluoride, but not in plants with too much boron in their tissues. The absence of chlorotic leaves in the begonias therefore could be cited as evidence for ruling out fluoride toxicity at least. But Marousky made his observations on Easter lilies which might show very different symptoms from begonias.

Elliott and Nelson (1981) report that *Begonia hiemalis* cv Schwabenland Red (Rieger begonia) will exhibit incipient symptoms of boron toxicity at concentrations of 125 to 258 ppm. The symptoms on *Begonia hiemalis* were chlorosis of the leaf margin progressing to necrosis extending 3-5 mm from the margin. These symptoms are not exactly the same as the ones observed on *Begonia lucerna*, but this may be due to the physical differences in the species. Schwabenland Red has small, dark, reddish, somewhat leathery leaves, whereas *Begonia lucerna* has large, deep green, thin leaves. It is difficult to rely on symptoms for the identification of boron toxicity since no specific function has been pinpointed for this element in plants. It is possible that the excess boron was supplied with superphosphate since Sauchelli (1960) reported that 8 ppm B was found in this fertilizer.

According to Kohl and Oertli (1961) boron tends to collect in leaves which are the terminus for the transpiration stream in which boron is probably passively carried. Therefore boron content is highest in the marginal areas, where the toxic effect also shows up. Due to the accumulation in leaves boron toxicity can build up, even when plants are supplied with normal amounts. It was indeed difficult to get rid of the symptoms in *Begonia lucerna* which are always grown from cuttings. The cuttings grown in Nutricote 14-14-14 showed much fewer symptoms, but the problem was alleviated only gradually. Some slight symptoms still turned up in the latest experiments in plants grown under higher temperatures and without lime amendments to the growing medium.

For the plants grown in the greenhouse the internode length on the branches of the main stem were significantly different (.05 level) from those for plants grown with 14-14-14 or with 18-9-9. The length of the cane internodes of plants in the greenhouse was also significantly shorter than that of plants grown with 14-14-14. The resulting short canes improved the appearance of the plants grown in the greenhouse, but the extremely short branches on the main stems and the lesions on the leaves made the plants grown in the greenhouse unsaleable.

Unamended and Limed Growing Media

Agricultural lime is supplied to relatively acidic growing media such as peat mixes, to reduce acidity and thereby increase the availability of phosphates, calcium, magnesium and molybdenum. Begonias are known to grow well in acidic media, i.e. at pH 4.5. This was found to be true for *Begonia lucerna* in early experiments, where media pH's of 4.5 to 6.5 were seen to be equally suitable for the species.

There was not much difference in plant development in limed (Treatment 4) and unlimed media (Treatment 5) in the warm growth chamber. There was no significant difference detectable between the internode lengths on the main stem of plants in any treatments in the growth chamber. But after ten weeks in the cool greenhouse the lengths of internodes in main stem branches were significantly greater (.05 level) in plants grown in the limed medium than in plants grown without lime. No canes had developed yet in either treatment. This may indicate that nutrients were indeed a limiting factor in the cool temperature because they were less available to plants (Joiner 1983). They were sufficiently available at the high, but not at the low pH to the plants with reduced metabolism under lower temperature, when the absorption rate of mineral elements is reduced, as is the permeability of membranes and the rate of cytoplasmic streaming (Janick, 1986). After four months, when the temperature had gone up again and when all nutrients could easily be taken up there was not much difference in the plants growing in the two media. It was observed that number and length of internodes in both media for plants grown for 4 months in the greenhouse were greater than those of plants grown in the growth chamber, where the temperature always was kept at 24 °C. This could indicate an earlier maturity of the tissues under higher temperature, which prevented the internodes from growing any further. In the case of *Begonia lucerna* the stems turn slightly woody with age and are then unable to elongate any more. This seems to be verified by the fact that the number and size of the internodes which developed on the later upcoming canes (or shoots from the root area) were still greater in the plants from the growth chamber. The acceleration of maturity in the growth chamber is also indicated by the earlier flowering.

The greater number of watery crescents on the leaves of plants grown without lime, particularly in the more growth promoting warm chamber may indicate that the damaging substance becomes less available to the plants with higher pH in the medium. It was found by Mengel and Kirkby (1978) (as reported by Joiner, 1983) that boron becomes less available for plant absorption with increasing pH. Another reason for the obvious relief brought about by calcium could be the detoxifying effect of calcium on micro-nutrient levels (Wallace, 1971; Joiner, 1983). Yet another reason could be that calcium is a constituent of the cell wall and is also found as calcium pectate in the middle lamella. In greater abundance it strengthens the cell walls.

The amount of other nutrients provided to the plants grown in limed and unlimed media seemed to be sufficient for the purpose of keeping the plants compact. A total of 1.05 g N from six applications of 15-30-15 and six applications of 20-20-20 was obviously adequate, although the weekly strength of 100 ppm and 75 ppm N is well below the recommendations of Nelson *et al.* (1978) for Rieger begonias. The differences in growth habit may explain the lower nutrient requirement. *Begonia lucerna*, when pinched, develops only two to three shoots from the main stem during the first weeks, and later one shoot from below the soil line. Rieger begonias develop many shoots and although they are small in some cultivars would need more nutrients because the plant mass is greater. This might not be clear at first glance, since *Begonia lucerna* appears to have more mass because of its large leaves. This makes them economical to produce, but on the other hand difficult because of the large leaves. It is not possible to just remove several leaves with blemishes, discoloration or breakage since each leaf contributes greatly to the overall form and appearance of the plant.

Nutricote 14-14-14 and Osmocote 18-9-9

Nutricote 14-14-14 has an advertised dissolution time of 3 months. Medium amended with this fertilizer promoted vigorous growth in *Begonia lucerna*. In the warm greenhouse it was found to provide enough nutrients for very lush and quick growth during the first two months. Then supplemental fertilizing had to begin with liquid 15-30-15 every second week

to keep the foliage at a good color and flowers plentiful.

The foliar level of nitrogen in the plants grown in 14-14-14 was 3.0% in the growth chamber and 2.7% in the greenhouse according to the chemical analyses. This is again lower than the values given for well grown Rieger begonias (4.85%) by Nelson *et al.* (1979). In the cooler greenhouse less nutrients would be released (Maynard and Lorenz, 1979) and growth was less lush, but still very vigorous.

Nutricote 14-14-14 is a very dependable fertilizer for *Begonia lucerna* to keep production time as short as possible. The plants were ready for sale, considering size and flowering, after 10 weeks. Growth retardants must be used, even at a slightly higher level than the 0.25 mg a.i. ancymidol which was used in these experiments, particularly because of the long canes. These canes, on the other hand, were not significantly different from the canes of plants grown with 0-20-0 or with lime amendment. This shows that long cane internodes were a problem in most treatments in the growth chamber. In the greenhouse as well main stem internodes of plants grown with 14-14-14 were not significantly longer than those grown with 18-9-9 or with lime amendment (all plants developed well). On the other hand, the canes of plants grown with 14-14-14 in the greenhouse were significantly longer than those of plants in lime-amended medium, which contained plants with the best shape.

Osmocote 18-9-9 was a disaster in the warm growth chamber since three of the five test plants died, the fourth barely survived and only one recuperated and started to grow and flower later. These plants were therefore not included in the statistical analysis. This fertilizer, which usually has a dissolution time of 8-9 months may have released far too high amounts of nutrients at the warm temperature. This result is not at all in accordance with reports in the literature where long-time slow release fertilizers are recommended for begonias (Maynard and Lorenz, 1979). These recommendations were made for Rieger begonias which probably need more nutrients, but the observed lack of new root growth should not have occurred since the temperature was not excessive for tropical plants for which slow release fertilizers are mainly produced. Maybe it is no coincidence that in rooting trials, reported elsewhere, (Marahrens and Toop, 1986), the only medium in which cuttings died was an

Osmocote 14-14-14 mix. There could be some substance in the coating of Osmocote which is specifically toxic to *Begonia lucerna* when it is used under high temperatures. Another possibility would be that the Osmocote had been improperly stored and consequently large amounts of nutrients were released at once. Since this fertilizer was kept on a shelf in the greenhouse the possibility of herbicide absorption cannot be excluded either.

The nitrogen content of these plants grown with 18-9-9 in the growth chamber exceeded that of healthy plants grown in the greenhouse by 1.5 times (4.8% in growth chamber plants compared to 2.7% in greenhouse plants). The fast developing plants grown with 14-14-14 from the growth chamber contained 3.0% N, those from the greenhouse 2.7% N. The phosphorus content was low compared to the nitrogen content at 0.26%, but it was the same as in healthy plants in other treatments. The nitrogen content was the same as found by Nelson *et al.* (1979), in healthy Rieger begonias, while the phosphorus content was much lower, since Nelson *et al.* report it at 0.6%. As pointed out earlier the requirements of the Rieger begonias may be considerably higher. The levels cited by various authors are somewhat on the high side generally, since Joiner (1979) cites many literature sources which indicate that in floricultural and foliage plants the nitrogen content should be 2.5 to 4.5% of dry weight and the phosphorus at 0.2 to 0.3% of dry weight.

Since the possibility exists that the 18-9-9 Osmocote released too much nitrogen compared to phosphorus for *Begonia lucerna* and since there were problems even in the cool greenhouse where less nutrients should be available this fertilizer cannot be recommended for this species.

Conclusion

The most important general results from these experiments were that *Begonia lucerna* needs long days for flowering and that light and fertilizer had a great influence on the development of growth retardant-treated *Begonia lucerna*.

A. Low light (12.7 W/m² PAR) of 16 h at 24 °C was sufficient for healthy development and good flowering, but induced strongly horizontal growth in plants on which growth retardants were effective.

B. Under high light (23.5 W/m² PAR), other conditions being equal, no abnormal horizontal growth occurred. Internode length for ancymidol-treated plants was much shorter under this high light than under low light.

1. Nutricote 14-14-14 amendment is a suitable treatment for the quick production of this species.

2. Osmocote 18-9-9 mix caused root problems, particularly in the warm growth chamber, where three out of five plants died.

3. In the 0-20-0 mix plants developed watery crescents, which later turned necrotic, on the leaf margins. These symptoms were probably due to boron toxicity.

4. Plants in the unlimed medium and provided with weekly liquid fertilizer also developed some small watery crescents.

5. In the limed medium provided with weakly liquid fertilizer plants developed very well.

C. In a greenhouse with supplemental HPS-light (total irradiance 16 to 66 W/m²) plants in the five treatments grew more slowly, and showed less detrimental reactions in treatments 2, 3, and 5 than comparable plants in the growth chamber.

As a result of this work *Begonia lucerna* is being marketed as a hanging basket plant today.

VI. Research: Other Begonia Species Screened for Suitability as Pot Plants

A. Introduction

In order to find more attractive *Begonia* species for pot plant cultivation 12 species were selected from the Begonia collection at the Agricultural University at Wageningen, Holland with the help of Dr. Doorenbos, a world authority on begonias. The cuttings were rooted and grown on in the U of A greenhouses and then shown at the regional meeting of Flowers Canada in Edmonton in the Spring of 1984. *Begonia sp. 1301*, *Begonia serratipetala* Irmscher, and *Begonia sp. 1302* attracted special attention from the growers and retailers present. Therefore, an attempt was made to find suitable techniques for rooting and mass producing clones of these species.

All three species have a natural compact growth habit that permits them to be handled easily without treatment with growth retardants. To begin with, all cuttings were grown in a shaded greenhouse in relatively low light and low temperature. After observation of the species under these conditions for slow development, they next were grown under conditions which encourage faster growth in hopes of reducing the production time. These conditions included higher temperature combined with supplemental HPS lighting in the greenhouse and both temperature control and high light intensity from fluorescent and incandescent sources in a growth chamber.

Pinching was only used to even out vertical and lateral growth in the two shrub-like species. The cane-like *Begonia species 1302* was not pinched because it developed several stems naturally. Pinching would prolong production time even more in this slow-growing species.

B. Materials and Methods

Descriptions of Plants

a) *Begonia sp. 1301* is still unnamed. It was collected in Costa Rica about 1977. This shrub-like species develops masses of hanging stems with dark green, shiny, serrate leaves which are 2-3 cm wide and 3-4 cm long. The flowers are greenish white and quite insconspicuous, about 0.5 cm in diameter, with only 3 to 4 flowers per cyme (Figure 17).

b) *Begonia serratipetala* Irmscher, a native of New Guinea is also a shrub-like species with shiny dark reddish, deeply lobed, serrated leaves and rose-pink flowers (Figures 18 and 19).

c) *Begonia sp. 1302* is a cane-like species which was found at a flower market in Mexico by Mrs. Millie Thompson of New York. It has pure white flower clusters and striking, large, white dots on its ovate oblique leaves. (Figure 20).

Propagation from Cuttings

a) Tip cuttings of the shrub-like species and tip and leaf-bud-cuttings of *Begonia sp. 1302* were placed in flats filled with 1) sand, 2) peat-vermiculite mix (1:1) amended with 2.89 kg lime, 0.765 kg 0-20-0, 2.25 kg calcium nitrate, and 0.545 kg potassium chloride per m^3 of medium.

b) Leaf cuttings of the three species were placed in flats of peat.

The flats were placed under a plastic tent in a shaded greenhouse during summer conditions of daylight. The temperature of the greenhouse was set at 21 °C, but the temperature under the plastic tent reached 28 °C at times.

Growing-on of Rooted Cuttings

a) After the cuttings had rooted 15 of each shrubby species and 9 of *Begonia species 1302* were potted singly into 12 cm plastic pots in unamended peat-vermiculite mix to which 100 mℓ of fertilizer solution at 200 ppm 20-20-20 was applied weekly. Fifteen rooted

cuttings of the shrubby species were potted singly in peat-vermiculite amended with 8.5 kg lime, 9.5 kg Nutricote 14-14-14 and 45 g fritted trace elements per m^3 of mix. Five pots of the shrubby species and 3 pots of *Begonia sp. 1302* from each treatment were placed in a completely randomised block at each of the following locations:

1. a shaded greenhouse at 19-23 °C and irradiance of 16-18 W/m^2,
2. a growth chamber at 24 °C and 16h light of 23.5 W/m^2 of which 18.8 $W/^2$ came from fluorescent and the remainder from incandescent sources,
3. A greenhouse at 18-22 °C under daylight, supplemented by HPS-lamps to 16.9 $W/^2$ on a dull day and 66.5 W/m^2 on a sunny day.

These experiments were repeated at least three times with each species. *Begonia serratipetela* was also grown in a growth chamber at 24 °C under only fluorescent lights radiating 19 W/m^2. *Begonia sp. 1302* was also grown in the shaded greenhouse in unamended medium with regular fertilizer applications of 20-20-20 at 100 ppm in solution.

Rooting

In sand all three species rooted slowly and looked constricted at the base of the stem. The roots were few and short. *Begonia sp. 1301* recovered after the cuttings were potted in the peat-vermiculite mix and developed a root mat of normal size. *Begonia serratipetula*, on the other hand, did not grow, but died after potting when the original rootsystem was small. *Begonia sp. 1302* survived on one or two developing roots, but grew very little and did not initiate more roots after potting.

In the peat-vermiculite mix cuttings of *Begonia sp. 1302* developed many strong roots and could be potted after 9 days without any visible shock or interruption of growth.

With *Begonia serratipetala* rooting was slow. It took 4 weeks for a good mat of fibrous roots to develop on the primary succulent roots. Cuttings potted up without such a mat did not grow satisfactorily and died some weeks later.

In *Begonia sp. 1302* not all cuttings developed roots, unlike the other species whose cuttings would all develop at least some roots eventually. Cuttings which did not root started

to rot at the cut. No more than three primary roots developed on cutting which did root. These roots were wiry and did not branch on the first 3-4 cm from their origin. Lower down each primary root developed a distinct fibrous mat of secondary roots.

Leaf cuttings in peat developed roots for *Begonia sp. 1301* and *Begonia serratipetala*, but not for *Begonia sp. 1302*. Little plantlets developed on the leaves of *Begonia sp. 1301* after 4 weeks and on the leaves of *Begonia serratipetala* after 8 weeks. The plantlets in both species developed a good root system for their size.

Growing-on

Begonia sp. 1301 developed well under both fertilizer regimes, but additional liquid fertilizer applications became necessary to preserve the deep green color after about 6 weeks. It also developed graceful, hanging stems when the pots were kept in the shaded greenhouse. Very full, large plants could be marketed 11 weeks after the cuttings were made.

In the greenhouse with supplemental HPS-light, the stems were very strong and upright at first, but later turned gradually downward making the plants somewhat wide. Production times was 9 weeks (Figure 17).

In the growth chamber the growth of this species was too lush with very soft succulent stems. Later the youngest branches lost their primary leaves.

Begonia serratipetala did not perform well in the shaded greenhouse (Figure 18). The species developed few long stems with long internodes (Table 8) and relatively little branching. The color of the leaves was green with purple dots. In the growth chamber *Begonia serratipetala* did not grow well either; the leaf margins on the older leaves became dry and the leaves finally abcised. In contrast to that the *Begonia serratipetala* plants in the greenhouse with supplemental HPS-light grew into bushy, attractive plants with dark red leaves (Figure 19). It took 12 weeks to produce marketable plants. Under fluorescent lights only, the leaves were even darker red, but the plants looked stunted with many branches and very short internodes (Table 8).

Begonia sp. 1302 only grew well, though slowly, in the shaded greenhouse in unamended medium (Figure 20). The stems on plants fertilized with applications of 100 mℓ 20-20-20 solution at 200 ppm appeared to be very succulent, whereas the stems of plants grown with fertilizer applications of 100 ppm 20-20-20 solution were tougher. In the other locations darkish blotches appeared close to the leaf margins. When these plants were placed under lower light the new developing leaves were healthy.

C. Discussion

Rooting

Begonias grow naturally under a canopy of trees. This means that fallen leaves and broken branches form a loose mat of organic matter in which begonia roots grow. Therefore, these plants are not able to develop good roots in hard to penetrate 'soils' nor nutrient-free sand.

In the peat-vermiculite mix tip cuttings of *Begonia sp. 1301* rooted extremely fast. Unrooted cuttings could, therefore, be stuck in the final pot right away if a grower is able to spare the room for the pots for the additional 9 days of rooting time. The procedure would save labour in potting.

Begonia serratipetala needs to develop a fibrous root mat before potting. Only the fine roots seem to be stimulated to branch further by the unavoidable root pruning that occurs when the plants are potted. When thicker roots were broken only a few fibrous roots developed on the primary root close to the stem. The reason for this could be the strong succulence of the primary roots which may cause a broken root to dry out.

Begonia sp. 1302 has to be potted into a relatively large pot because of the distinct root mats developing low on each primary root. Transplanting shock is no problem for this species in peat-vermiculite medium because the roots are wiry.

Begonia 1301 and *Begonia serratipetala* can easily be propagated from leaves. The subsequent plantlets develop an excellent shape with many small stems. Of course,

production time is longer than from terminal cuttings, 4 months for *Begonia sp. 1301* and 6 months for *Begonia serratipetala*.

Growing-on

Begonia sp. 1301 is very quickly produced. No problems turned up in the greenhouse compartments, whether or not the shaded daylight was supplemented with HPS-lamps. The width of the plants grown under supplemental light could be reduced by switching off the lights for some days before the plants were prepared for shipping. On the other hand, plants grown under the supplemental light could be marketed much earlier as upright plants and thereby make them easily to handle in transit. If this procedure were followed a note should accompany the erect plants, pointing out that under low light the plants will develop a trailing habit.

Begonia serretipetala in the shaded greenhouse developed the typical features of plants grown under low light: long internodes, little branching and minimal red coloration (Kasperbauer, 1971; Tucker and Mansfield, 1972; Salisburg and Ross, 1985). The problem in the growth chamber with necrotic leaf margins must be related to the heat from the incandescent lamps because these symptoms did not develop at the same temperature setting under fluorescent light alone.

Very short internodes developed under fluorescent lights alone because of the total absence of FR in this spectrum (Smith, 1982). The strong red colour of the leaves was due to anthocyanin pigments which are synthesized at a higher rate under high light. Although the action spectra for anthocyanin production vary considerably among species, blue is known to be effective in nearly all species (Salisbury and Ross, 1985). Since fluorescent light contains a high proportion of blue in its spectrum this could be triggering the high rate of anthocyanin synthesis.

Begonia species 1302 does not tolerate growing conditions which accelerate development (forcing). On the other hand, the fact that it has to be grown under low light and at temperatures common in our homes makes it an easy to maintain houseplant.

D. Conclusion

The results of the screening were reported at a meeting of the WCSH in Calgary in the Spring of 1985 (Marahrens and Toop, 1985). As a consequence of this work cuttings of *Begonia sp. 1301* were requested by two large plant propagating firms. At least one of these growers produces that species commercially today.

VII. Tables

Table 1. Efficiency of 55% Saran Shade Mesh

	Irradiance total (mW/m^2)	Irradiance in bands $\mu W/m^2/nm$		Ratio
		Red	Far-Red	R:FR
Unshaded	23,770	490	330	1.48
Shaded	12,770	210	150	1.40
Shaded/ unshaded		42%	45%	

Table 2: Soil Drenches of Ancymidol (A-1 to A-3) and Chlormequat (C-1 to C-3)

Treatment	Chemical	Solution (ml/pot)	A.i. (mg/pot)
A-1	Ancymidol	120	0.22
A-2	Ancymidol	120	0.25
A-3	Ancymidol	120	0.32
C-1	Chlormequat	100	165
C-2	Chlormequat	100	212
C-3	Chlormequat	100	260
Control	Water	100	0.0

Table 3. Internode Number and Length, and Flowering under 16 h Days

Treatment	Main stem branch internodes		Cane internodes		Flowers	Comments
	no./shoot	av. cm	no./shoot	av. cm	no./shoot	
Control	4.9	5.1	5.0	7.8	0.8	weak stems
A-1	5.2	3.3	4.4	3.6	1.3	long stems
A-2	5.3	2.8	4.5	3.0	1.3	compact
A-3	6.3	2.4	5.3	2.7	1.0	compact
C-1	5.2	3.8	3.2	2.4	1.1	long stems
C-2	5.0	3.7	5.0	4.3	1.5	long stems
C-3	5.1	3.4	5.2	3.6	1.5	somewhat open

Main stem branch internodes: Ancymidol linear trend**
Chlormequat linear trend**
Ancymidol vs. chlormequat**

Cane internodes: Ancymidol linear trend*
Chlormequat linear trend N.S.

*, ** F-value for comparison of trend was significant at the 0.05 or 0.01 level, respectively.

N.S. = not significant

Table 4: Internode Number and Length, and Flowering under 9 h Days

Treatment	Main stem branch internodes		Cane internodes		Flowers	Comments
	no./shoot	av. cm	no./shoot	av. cm	no./shoot	
Control	6.5	4.8	5.0	5.9	0.1	weak stems
A-2	4.5	1.4	3.0	1.3	0.1	too compact
C-3	5.8	4.7	5.0	4.6	0.1	tall, leggy
$LSD_{.05}$	—	0.9	—	2.0	—	
$LSD_{.01}$	—	1.4	—	—	—	

Table 5: Average Internode Number, Length, and Flowering from Tip Cuttings Grown at 24 °C (23W/m²) for Ten Weeks after Potting

Treatment	Main stem branch internodes		Cane internodes		Flowers	Comments
	no./shoot	cm	no./shoot	cm	no./shoot	
1	4.6	1.85	5.8	3.04	1.6	tall cane
2	2.0	1.40	3.0	1.50	1.5	3/5 dead
3	3.7	1.88	4.8	2.63	0	B-toxicity
4	3.0	1.60	5.0	2.70	1.4	good
5	3.7	1.62	5.6	1.97	0.2	B-toxicity

Main stem internode length: N.S.

Cane internode length: $LSD_{.05} = 0.9$

Table 6: Average Internode Number, Length, and Flowering from Tip Cuttings Grown at 19 °C (±3 °C) (16 to 66 W/m²) for Ten Weeks after Potting

Treatment	Main stem branch internodes		Cane internodes		Flowers	Comments
	no./shoot	cm	no./shoot	cm	no./shoot	
1	3.35	1.80	3.7	3.13	0.2	best, tall
2	2.72	1.56	2.6	1.26	0	1/5 dead
3	2.40	1.04	3.25	1.96	0.2	B-toxicity
4	2.54	1.28	bud	bud	0.2	young
5	1.75	1.12	bud	bud	0	young

Main stem internode length: $LSD_{.05} = 0.5$

Cane internode length: $LSD_{.05} = 1.0$

Table 7: Average Number, Length, and Flowering of Leaf Bud Cuttings Grown at 19 °C (±3 °C) (16 to 66 W/m²) for Ten Weeks after Potting

Treatment	Main stem branch internodes		Cane internodes		Flowers	Comments
	no./shoot	cm	no./shoot	cm	no./shoot	
1	2.4	0.95	2.5	1.5	0	very young
2	3.0	1.03	2.2	0.96	0	very young

Main stem internode length: N.S.

Table 8: Results of Chemical Analysis of Tissues of *Begonia lucerna* Grown in Variously Amended Media

Treatment	Content of Elements in Plant Tissue						
	In Growth Chamber				In Greenhouse		
	N(%)	P(%)	B(ppm)	F(ppm)	N(%)	P(%)	B(ppm)
1	3.0	0.23	40	98	2.7	0.26	31
2	4.8	0.26	45	48	2.7	0.27	23
3	2.1	0.20	375	98	2.8	0.20	83
4	2.7	0.42	50	64	2.3	0.37	26
5	3.0	0.28	44	112	2.7	0.23	29

Table 9: Influence of Light on *Begonia serratipetala*

Light source	Irradiance (W/m^2)	Temp. °C	Int. length av. cm.	Leaf color	Flowering
1) Fluorescent	19	24	1.6	dark red	little
2) Fluores. & incand.	23	24	3.1	dark red	good
3) Day & HPS	16 - 66	18 -22	3.3	dark red	good
4) Shaded daylight	16 - 18	18 - 22	5.3	green	none

VIII. Figures

Figure 1: Untreated control plant in walk-in chamber at 12.7 W/m², 16 h days

Figure 2: Treatment C-1 at 165 mg (a.i.) chlormequat/pot in walk-in chamber at 12.7 W/m², 16 h days

Figure 3: Treatment C-3 at 260 mg (a.i.) chlormequat/pot in walk-in chamber at 12.7 W/m², 16 h days

Figure 4: Treatment A-1 at 0.22 mg (a.i.) ancymidol/pot in walk-in chamber at 12.7 W/m², 16 h days

Figure 5: Treatment A-2 at 0.25 mg (a.i.) ancymidol/pot in walk-in chamber at 12.7 W/m², 16 h days

Figure 6: Treatment A-3 at 0.32 mg (a.i.) ancymidol/pot in walk-in chamber at 12.7 W/m², 16 h days

Figure 7: Treatments A-2 and control in cabinet at 22.8 W/m², 9 h days

Figure 8: Treatments A-2 and C-3 in cabinet at 22.8 W/m², 9 h days

Figure 9: Leaf epinasty in *Begonia lucerna*, grown under daylight and 16 h incandescent light

Figure 10: Tip cuttings grown with Osmocote 18-9-9 in chamber at 24 °C and 23 W/m² (left), in greenhouse at 19 °C and 16 to 66 W/m² (right)

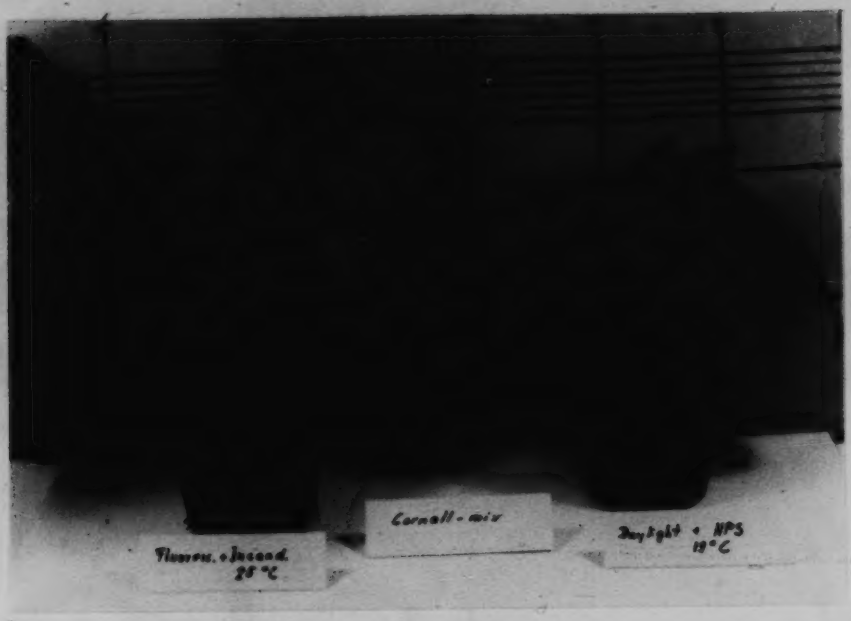

Figure 11: Tip cuttings grown with 0-20-0
in chamber at 24 °C and 23 W/m² (left),
in greenhouse at 19 °C and 16 to 66 W/m² (right)

Figure 12: Tip cuttings grown with lime in medium
in chamber at 24 °C and 23 W/m² (left),
in greenhouse at 19 °C and 16 to 66 W/m² (right)

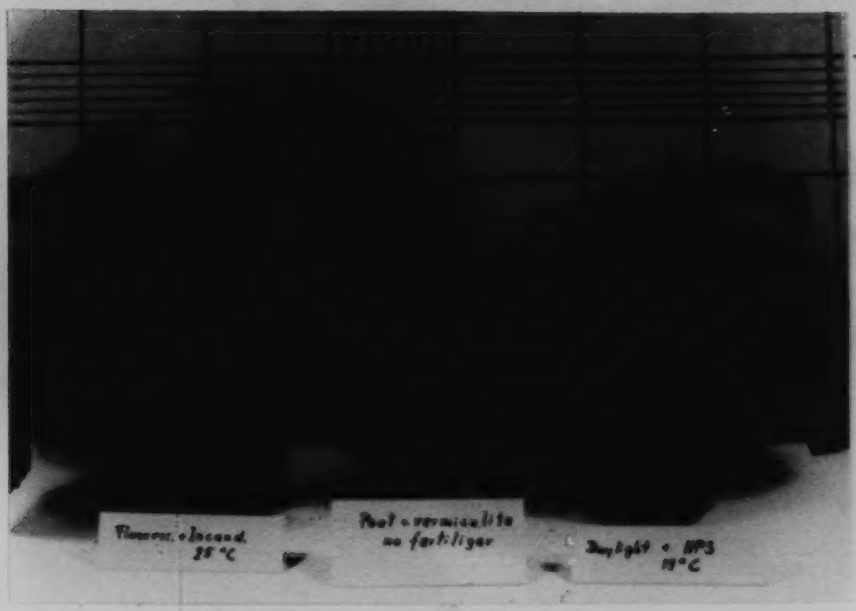

Figure 13: Tip cuttings grown without amendment in chamber at 24 °C and 23 W/m² (left), in greenhouse at 19 °C and 16 to 66 W/m² (right)

Figure 14: Tip cuttings grown with Nutricote 14-14-14 in greenhouse at 19 °C and 16 to 66 W/m² (left), in chamber at 24 °C and 23 W/m² (right)

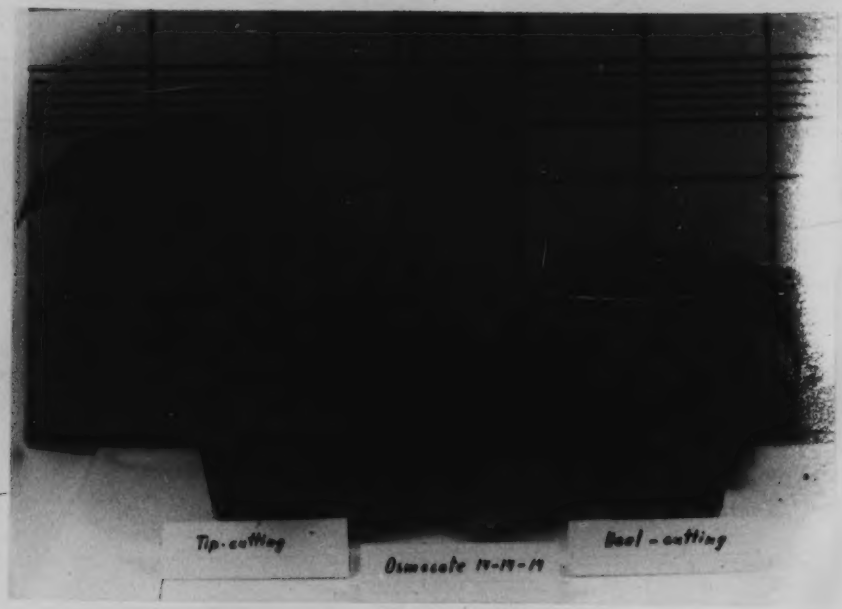

Figure 15: Tip cutting (left) and leaf bud cutting (right), grown with Nutricote 14-14-14 in greenhouse at 19 °C and 16 to 66 W/m²

Figure 16: Tip cutting (left) and leaf bud cutting (right), grown with Osmocote 18-9-9 in greenhouse at 19 °C and 16 to 66 W/m²

Figure 17: *Begonia sp. 1301* grown in a greenhouse at 19 °C and 16 to 66 W/m² from tip cuttings, 11 weeks (front), 4 weeks (left) after potting

Figure 18: *Begonia serratipetala* grown in a shaded greenhouse at 16 to 18 W/m², 16 weeks after potting

Figure 19: *Begonia serratipetala* grown in a greenhouse at 19 °C and 16 to 66 W/m², 16 weeks after potting

Figure 20: *Begonia sp. 1302* grown in a shaded greenhouse at 16 to 18 W/m², 16 weeks after potting

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Appendix 1: Preliminary Experiment to Establish Effectiveness of Growth Retardants on Begonia lucerna

In order to find out which of the commonly available growth retardants daminozide, chlorphonium, chlormequat, and ancymidol reduced internode length of *Begonia lucerna* 25 rooted cuttings were grown, one plant per pot, from December 1982 for 5 weeks in a 2:1:1 soil:peat:perlite mix which had been watered with 200 mℓ (200 ppm) of 20(N)-20(P_2O_5)-20(K_2O) solution. The pots were kept in a greenhouse compartment at 19 °C and were provided with 16 h supplemental lighting from incandescent 150 W bulbs, spaced 80 cm apart and kept at a distance of 1.20 m above the plants.

a. Five plants were sprayed with 0.5% daminozide solution to run-off (as recommended by the manufacturer for poinsettias and other pot plants).

b. Five plants each were drenched with 0.176 g (a.i.) chlorphonium (which was recommended for Easter lilies, whereas the dose recommended for other pot plants was much lower).

c. Five plants each were drenched with 295 mg (a.i.) chlormequat, (the recommended amount to produce compact poinsettias and azaleas).

d. Five plants each were drenched with 0.22 mg (a.i.) ancymidol, (which is the recommended rate for chrysanthemum, poinsettias and Easter lilies).

e. Five plants each were drenched with 100 mℓ distilled water as control plant.

The pots were kept in a totally randomized design and re-randomized each week.

Chlormequat and ancymidol reduced internode length and plant height in *Begonia lucerna*. The control plants, as well as the plants treated with chlormequat and ancymidol showed leaf epinasty and a slight forward bending of the stems (Figure 9). Several plants developed unsightly spots of mildew on stems and/or leaves. Therefore it was decided to eliminate the soil from the growing medium in order to eliminate the pathogen.

Results

Table 10: Effectiveness of 4 Growth Retardants on Average Internode Length of *Begonia lucerna*

Treatment	Height in cm	Int. Length in cm.
Control	28.0	3.3
Daminozide	28.3	3.7
Chlorphonium	30.0	3.8
Chlormequat	15.0	1.9
Ancymidol	20.0	2.6

Appendix 2: The Effect of Pinching to 2, 3 or 4 Nodes on Subsequent Development of Begonia lucerna

Fifteen rooted cuttings of *Begonia lucerna* were placed in a greenhouse without humidity control. Fifteen rooted cuttings were placed in a growth chamber with 60% r.h.

In each location:

5 plants were pinched above the second,

5 plants above the third, and

5 plants above the fourth visible node.

Two weeks after pinching all plants were treated with ancymidol.

Results

On the plants pinched above the fourth node in the greenhouse only one developed every axillary bud into a shoot (main stem shoots). In the growth chamber 3 out of the 5 plants developed all four main stem shoots. The second buds from the top developed the least, whereas the uppermost buds developed faster than the lower ones. This gave these plants an elongated and sparse appearance.

On the plants pinched above the second or third node every bud developed into a shoot in both locations. In addition to these main stem shoots a vigorously growing shoot (cane) developed from the lowest bud on the stem, which had been buried in the potting process. The internodes of these canes were longer than those of main stem shoots, but were still shorter than internodes on canes of untreated plants.

After 4 to 5 months of developmental growth another cane developed from an adventitious bud below the soil line on 7 out of 10 plants. The internodes of these canes were extremely long, up to 10 and 12 cm each.

Appendix 3: The Effect of Various Rates of Growth Retardants on Begonia lucerna Plants Grown in 0-20-0 Mix Under Daylight Supplemented by Incandescent Photoperiodic Lighting

Twenty-five rooted cuttings were singly potted in a 1:1 peat-vermiculite mix, amended per m^3 with 2.85 kg agricultural lime, 1.25 kg 0-20-0, 0.60 kg 14-0-44, and 0.06 kg fritted trace elements. After 3 weeks the plants were pinched to 3 nodes and 2 weeks later they were treated with growth retardants. The pots were placed in a shaded greenhouse which was supplemented with incandescent lamps to bring the photoperiod up to 16 h. Every second week 100 mℓ 20-20-20 at 200 ppm was applied.

Results

Three months after potting the plants looked somewhat yellowish-green and had developed watery areas on the margins of older leaves. These areas dried into papery necrotic crescents.

The average lengths of internodes of the variously treated plants were as follows: 0.20 mg ancymidol per pot resulted in 2.47 cm, 0.25 mg ancymidol per pot resulted in 2.14 cm, 165 mg chlormequat per pot resulted in 2.65 cm, 212 mg chlormequat per pot resulted in 2.51 cm, 120 g water per pot resulted in 4.00 cm long internodes.

Follow-up experiments in which the plants were grown in the same medium except a doubled and tripled content of agricultural lime initially resulted in fewer watery spots, but later showed similar symptoms as the plants grown with less lime.

Appendix 4: Effect of Growth Retardants Combined with Low Light on Growth Response of Begonia lucerna

In response to a suggestion from the Cecil Delworth Foundation *Begonia lucerna* plants were grown in 5 hanging baskets. Four rooted cuttings per basket were placed as horizontal as possible, so that the stems touched the rims of the container and the roots of all plants met in the middle of the containers. Two baskets were drenched with chlormequat (212 mg/plant) two with ancymidol (0.25 mg/plant), and one with water (control). All baskets were hung in a shaded greenhouse at 16 to 18 W/m^2 natural light.

Results

On the control plants the tips of the horizontally placed stems grew upward in a negatively gravitropic direction. Morevoer, the most vigorous growth occurred in canes which developed from lower axillary buds on the bent part of the stem. No flowers developed on the four plants.

In all plants treated with growth retardants the tips of the horizontally placed stems went on growing straight, without changing the angle of growth. The developing axillary buds grew out plagiotropically at about 45°. It was only after 4 to 5 months that some canes from adventitious buds below the soil line developed and grew straight upward. All plants treated with growth retardants flowered profusely.

Appendix 5: Effect of Small Pots on the Development of Begonia lucerna Plants

Plastic pots of 10 cm diameter rather than the usual 12 cm size were used as a means of limiting root size and with it the capacity of plants to take up nutrients. Ten rooted cuttings were potted in individual 10 cm plastic pots with a peat-vermiculite mix amended with lime and Nutricote 14-14-14 (Treatment 1, chap. V). The plants were pinched and treated with 0.25 mg a.i. ancymidol. Five pots were kept in a shaded greenhouse with supplemental incandescent light, five pots were placed in a growth chamber at 24 °C under 12.7 W/m^2 of mixed light. From the fifth week after potting bi-weekly applications of 20-20-20 fertilizer solution (220 ppm) were made using 100 mℓ per pot.

Results

All plants in both locations developed weak stems which did not stand up. Older leaves were yellow and often abscised; the younger leaves showed a reddish tinge. The plants grown in the growth chamber showed slightly less discoloration, but not one plant in this experiment was of marketable quality.

Appendix 6: Effect of Various Fertilizer Treatments on the Development of Begonia lucerna Plants

In order to find out whether the long term (9 months) slow release fertilizer Osmocote 18-9-9 was suitable for the production of *Begonia lucerna* the following experiment was conducted in a greenhouse without supplemental light, starting May 1984. Fifteen rooted cuttings were potted into peat-vermiculite mix containing Osmocote 18-9-9, 5 cuttings in the same medium amended with Nutricote 14-14-14, 5 cuttings in the medium amended only with lime, but watered with 20-20-20 solution. (Media are described in chap. V). No further fertilizer was added for 2 months. The plants were pinched to 3 nodes and treated with 0.25 mg (a.i.) ancymidol.

Results

The plants flowered well and were very compact with average internode lengths of 1.35 cm in the 14-14-14 amended mix, 1.86 cm in the 18-9-9 amended mix, and 1.01 cm in the limed medium plus liquid fertilizer treatment. All plants had a low number of shoots developing per plant. The average number of branches on the main stem and the average numbers of canes (in brackets) were: 1.8 (1.0) in the 14-14-14 mix, 1.4 (0.6) in the 18-9-9 mix and 1.8 (0.8) in the limed medium watered with 20-20-20 solution.